

Open Research Online

The Open University's repository of research publications
and other research outputs

Assessing the global conservation status of ecologically poorly undertood, threatened chelonian species : the case of the critically endangered Madagascar spider tortoise (*Pyxis arachnoides*)

Thesis

How to cite:

Walker, Ryan Campbell James (2012). Assessing the global conservation status of ecologically poorly undertood, threatened chelonian species : the case of the critically endangered Madagascar spider tortoise (*Pyxis arachnoides*). PhD thesis The Open University.

For guidance on citations see [FAQs](#).

© 2012 The Author



<https://creativecommons.org/licenses/by-nc-nd/4.0/>

Version: Version of Record

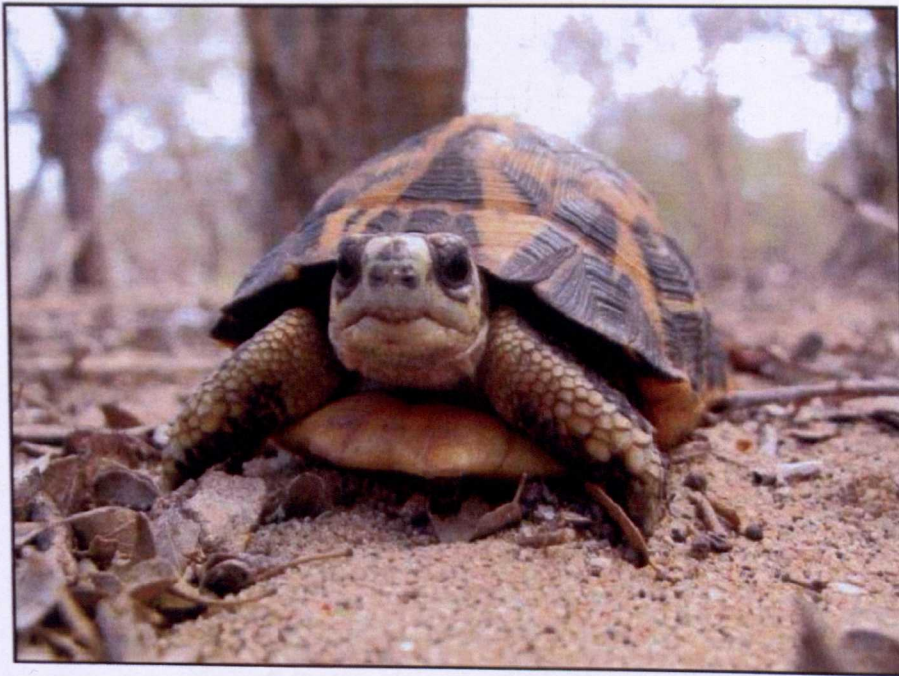
Link(s) to article on publisher's website:

<http://dx.doi.org/doi:10.21954/ou.ro.0000d4f5>

Copyright and Moral Rights for the articles on this site are retained by the individual authors and/or other copyright owners. For more information on Open Research Online's data [policy](#) on reuse of materials please consult the policies page.

oro.open.ac.uk

**Assessing the Conservation Status of Ecologically Poorly Understood,
Threatened Chelonian Species; the Case of the Critically Endangered
Madagascar Spider Tortoise (*Pyxis arachnoides*)**

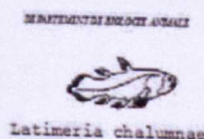
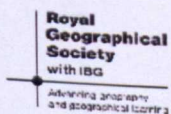
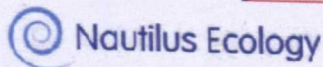


Submitted by:

Ryan Walker BSc (Hons), MSc, CEnv

Department of Environment, Earth and Ecosystems, The Open University

For consideration for the qualification of PhD, December 2011



Date of Submission: 3 January 2012
Date of Award: 7 November 2012.

APPENDIX NOT COPIED
ON INSTRUCTION FROM
UNIVERSITY



This work is dedicated to the many Malagasy nationals who tirelessly work towards to the preservation of the remaining, yet greatly threatened natural heritage of their biologically and culturally fascinating island nation¹.



¹ Cover photo: *Pyxis arachnoides arachnoides* Tsimanampetsotsa National Park, southwest Madagascar. Photo above: the author with field staff from Madagascar National Parks and the Madagascar Biodiversity Partnership. Photo credit; RCJ Walker.

Abstract²

The IUCN Red List for Threaten Species is widely regarded as the authority for assessing a particular species conservation risk. However, this process has come under some criticism for designating species as high conservation risk on a precautionary principle, using limited data, grey literature or anecdotal information. The Madagascar spider tortoise (Pyxis arachnoides) is one such species, up-listed from Vulnerable to Critically Endangered status, based on data of limited spatial resolution and anecdotal information, suggesting risk from poaching and habitat loss, resulting in significant reduction in population size, thus allowing the criteria of Critically Endangered to be met (A4cd; E). This study assesses these risks to the species at a range wide level, using presence/absence surveying and incorporating data into a geographical information system to describe distribution contraction within differing areas of land use. This was coupled with a line transect distance sampling procedure to assess real time population size within the current area of occupancy. A Mark-Capture-Recapture, Cormack-Jolly-Seber model and a stage class, projection matrix was developed to model mean annual survival, finite growth rate and population survival. Finally, remotely sensed habitat loss was monitored within the core of the species range. These data suggest that the species has suffered a reduction of 70.8% from suspected historical extent of occurrence to the current area of occupancy, now inhabiting a total area of 2,463.8 km², with 73.5% of the current distribution occurring within existing or proposed protected areas. Range wide population density equals 226.9 (95% CI 168.1-306.3) tortoises km⁻², with a total global population estimate of 664,980 (95% CI. 492,680-897,550). Adult mean annual survival is 0.82 (SE± 0.15), however juvenile survival cannot be modelled due to low recapture. There is an actual mean population decline of 10.8%, coupled with mean forest loss of 1.2% yr⁻¹ (2003-2011), within the core of the range. The projection matrix model reveals finite population growth to be $\lambda=0.983$, indicative of a c. 1.4% decline annually, with adult survival the most sensitive parameter to population survival. Projection modelling suggests the species will probably become ecologically non-viable in approximately 170 years. Results confirm the species IUCN Critically Endangered status. Development programs and tighter protected area management are required to address the poverty induced drivers threatening this species. This assessment provides an ideal model for similar dry forest tortoise species suffering status data deficiency. The author proposes a temporary five year condition to be placed on the designation of species considered to be of high conservation concern, similar to this species, up-listed on the Red List using anecdotal information or grey literature, whilst funds are secured and empirical peer reviewed data is obtained to confirm the status in the wild.

² This thesis has been formatted in accordance with the OU Research Degree Examination Guidelines and the authors instruction of the journal *Oryx*

Contents

Chapter 1: Introduction 11

Chapter 2: Conservation of the Madagascar Spider Tortoise (*Pyxis arachnoides*) amid
changing land use policy: Assessing the spatial coincidence of relict populations
within protected areas and mining concessions' 23

 Introduction 23

 Methods 25

 Results 32

 Discussion 37

Chapter 3: Global population estimate of the Critically Endangered Madagascar spider
tortoise (*Pyxis arachnoides*) 42

 Introduction 42

 Methods 44

 Results 51

 Discussion 54

Chapter 4: Survival probability of a population of Madagascar spider tortoises (*Pyxis
arachnoides*) 58

 Introduction 58

 Methods 59

 Results 63

 Discussion 63

Chapter 5: The effect of habitat deterioration on the long term survival of the Critically
Endangered Madagascar spider tortoise (*Pyxis arachnoides*) 66

 Introduction 66

 Methods 68

 Results 75

Discussion 77

Chapter 6: Discussion..... 83

Acknowledgments..... 93

References.....96

Appendix 1.

Peer review publications resulting from the PhD research.... .123

Appendix 2.

Popular articles resulting from the PhD research.....131

Figures

Figure 1: Suspected historical extent of occurrence of the three subspecies of spider tortoise as described by Bour, (1981) and Pedrono (2008), grey areas denote vegetation cover derived from LandSat TM7 imagery (Harper et al., 2007). Northern block (clear) denotes suspected area occupied by *P. a. brygooi*; with image of the subspecies' typically associated Mikea forest habitat (a); middle block (diagonal hatch) denotes suspected area occupied by *P. a. arachnoides* with image of typically associated dry southern forest habitat (b); southern block (cross hatch) denotes suspected area occupied by *P. a. oblonga* with the image of the typically associated coastal dune habitat/dry southern forest habitat of the extreme south. Photo credit: RCJ Walker ... 19

Figure 2: typical morphology of *P. a. oblonga* showing dark plastral edge pigmentation (top left) and mobile plastral hinge allowing for full retraction of head and front legs (top right); *P. a. arachnoides* supports a semi mobile hinge (middle right and middle left) and *P. a. brygooi* typically displays a rigid plastral hinge (bottom right and bottom left). Photo credit: top left, top right, middle left, middle right, bottom left; RCJ Walker, bottom right; I Smith..... 20

Figure 3: Google Earth image of a section of the survey area within the Manombo River discharge point, southwest coastal Madagascar. The dark line delineates an area of classified intact habitat to the north of the line that was selected for surveying, with degraded classified land south of the line characterized by parcels of agriculture and livestock corrals. These high resolution images were also used in conjunction with the Landsat imagery to identify the limits of the polygon boundaries for parcels of habitat

that support tortoise populations and to identify areas of degraded habitat and areas devoid of tortoises..... 27

Figure 4: Suspected historical extent of occurrence for the three subspecies of spider tortoise described by Bour, (1981) and Pedrono (2008), with *P. a. brygooi* to the north, *P. a. arachnoides* to the middle of the range and *P. a. oblonga* to the south of the range with corresponding photos illustrating the varying plastron morphologies (Chapter 1). Vegetation cover layer is represented in grey and 131 field survey points are overlaid into the GIS. Photo Credits: RCJ Walker 29

Figure 5: Spatial distribution of existing or proposed protected areas under the Madagascar Protected areas expansion program (green cross hatch) and sites proposed under the Madagascar Mining Code for mineral extraction (red cross hatch) within southwest Madagascar. 30

Figure 6: Current area of occupancy of the three subspecies and two intergrade populations of spider tortoise displayed in black (central map); A=*P. a. brygooi*; B= *P. a. brygooi*/*P. a. arachnoides* intergrade population; C=*P. a. arachnoides*; D= *P. a. arachnoides*/*P. a. oblonga* intergrade population; E = *P. a. oblonga*. Blow out maps represent corresponding populations in relation to the proposed/existing protected areas displayed in green cross hatch and areas of proposed mineral extraction displayed in red cross hatch. (a) The point represented by the star to the north of *P. a. arachnoides*' area of occupancy represents the remnant population missed by the survey, reported by (Scott et al. 2008). (b) The star to the east of *P. a. arachnoides*' area of occupancy represents the individual tortoise missed by the survey, reported by Rick Hudson (Pers. comm.). 33

Figure 7: The 64 survey points displayed in addition to the current area of occupancy shown as eight areas of forest known to be occupied by *P. arachnoides* as described by Walker et al, in press and Walker (2010) (Chapter 2). A= three sub populations of *P. a. brygooi*, B= 1 sub population of *P. a. brygooi/P. a. arachnoides* intergrades, C= 1 sub population of *P. a. arachnoides* D= 1 sub population of *P. a. arachnoides/P. a. oblonga* intergrades, E= 2 sub populations of *P. a. oblonga*, showing a very narrow area, occupied to the east of the range (blow out). 45

Figure 8: Raw distance data for the entire population of *P. arachnoides* grouped into 50cm intervals showing over recording at 151-300cm, and a spike at 0cm distance as a result of varying detection probability further from the centre line due to variation in habitat complexity and the small size of the species. 50

Figure 9: Data detection probability $g(y)$ for data comprising the entire population of *P. arachnoides* after truncation and transformation of data to intervals using Program Distance 5.0 for the half-normal + hermite polynomial model. 51

Figure 10: Mean number of minutes during three time intervals (0630h-1030h, 1030h-1530h and 1530h-1830h) when nine individual tortoises were hidden to the observer. 52

Figure 11: Study site 3km east of the coastal community of Anakao within the core of the species range, within the coastal dry forests of southwest Madagascar. *P. arachnoides* range is represented in black. 60

Figure 12: (a) Study site within the core of *P. arachnoides* coastal dry forest range, southwest Madagascar. Range map showing current area of occupancy adapted from Walker & Rafeliasoa, (2012) against the former historical extent of occurrence (Bour, 1981). (b) fifteen survey quadrats demarked by black dots overlaid on IKONOS 2 forest

cover data for 2003 and 2009, livestock corrals and patches of land cleared for cultivation can clearly be seen as pale patches compared to the darker areas of natural vegetation..... 69

Figure 13: Life-history diagram of *P. arachnoides*. Where G_i = annual probability of surviving and recruiting into the next size class, P_i = annual probability of surviving and staying within the same size-class and F_i represents the annual production rate of female offspring per adult female..... 74

Figure 14: Results of the decline projection for the *P. arachnoides* population within the coastal dry forests of the Anakao region. The solid line represents the projected decline through to the year 2150. The dots represent the true mean population density values for the tortoise population for years 2003, 2009, 2010 and 2011..... 76

Tables

Table 1: Current area of occupancy displayed against the suspected extent of occurrence documented by Bour (1981) and Pedrono (2008)†, in addition to the extent of these ranges for each population of tortoise that fall within existing or proposed protected areas or sites of proposed mineral extraction.....	35
Table 2: Current known area of occupancy of the three subspecies and two intergrade populations of the spider tortoise (<i>Pyxis arachnoides</i>) in Madagascar (Fig. 1), with the subpopulations indicated by the letters A–E, which correspond to the locations labelled in Fig 1, the source of these data, and the number of transects used to survey each subspecies and intergrade population and the years in which the surveys took place....	47
Table 3: Each of the four Distance models used to estimate the whole population of spider tortoises, with corresponding ΔAIC , mean density per km^{-2} (with upper and lower 95% confidence limits), mean population size (with upper and lower 95% confidence limits) and % coefficient of variation (% CV).	53
Table 4: Real and surrogate data for the construction of the <i>P. arachnoides</i> matrix. †= calculated mean survival from 16 surrogate species of chelonian taken from Pike et al. (2008)....	72
Table 5: Mean density of <i>P. arachnoides</i> for the three life stage classes across the 15 1 ha. survey quadrats within the coastal dry forests of Anakao for 2003, 2009, 2010 and 2011.....	75
Table 6: Results of regression analysis of <i>P. arachnoides</i> age class verses year (2003, 2009, 2010 and 2011).	76
Table 7: Stage-class projection matrix elements for <i>P. arachnoides</i> and associated sensitivities and elasticities.	76

Chapter 1: Introduction

There are many short comings in the knowledge of the basic ecology, taxonomy and conservation status of many rare or threatened species (Gaston, 2003; Brito, 2010). This lack of knowledge is often the greatest challenge facing conservation biologists when planning conservation management strategies (Brooks et al., 2006). These knowledge gaps can be wide ranging and authors and institutions have used a number of descriptions to detail the precise areas in knowledge gaps within species conservation biology. For example, the ‘Linnean shortfall’ can be used to describe the gap in global taxonomic knowledge, whereby only approximately 2 million of the possible 30 million species inhabiting the earth are described by science (Novotny et al. 2002; Mace et al. 2003). At a taxonomic level this problem can be illustrated when one considers that only approximately 50% of the amphibians discovered within Madagascar have been adequately described, with a further approximately 250 species still awaiting correct taxonomic description (Vieites et al., 2009), causing a huge Linnean shortfall for this taxon within this unique bioregion.

The ‘Wallacean shortfall’ has been used to describe the lack of the knowledge of the geographical range and abundance of a species (Brown & Lomolino, 1998), with these data and their subsequent rate of change being one of the most important aspects of conservation status assessments (McGowen et al., 1998). The current rates of species description averages approximately 15,000 species per year (Stork, 1993), however only 61,914 species have had their conservation status assessed against the IUCN Red List for Threatened Species and of these 8,641 are considered ‘Data Deficient’ (i.e., information is insufficient to make a conservation status assessment) (IUCN, 2012). However, despite these high levels of data deficiency amongst certain species within the IUCN Red List there has still been a high incidence of assigning

species within the IUCN Red List on a precautionary basis, as a result of assessments carried out using anecdotal information or unavailable grey literature, without use of sufficient peer reviewed and published, real time, empirical field data to confirm the current actual status of the species in question. This is often the greatest criticism of the Red Listing process (Mrosovsky & Godfrey, 2008); for example Seminoff & Shanker (2008) reviewed three sea turtle Red List assessments produced since 2002 and found that between 46 and 51% of all citations were from grey literature. Adding citations of personal communications or unpublished data to grey literature citations resulted in 68-80% of citations from non published literature. In addition to this, Mrosovsky & Godfrey (2008) suggest that up to 40% of assessments for other taxa, other than sea turtles consist of grey literature and/or personal communications. However, IUCN state that a lack of robust data should not deter attempts at applying the criteria to species (IUCN Standards and Petitions Subcommittee, 2010), which has caused some conservation biologists to bring into question the validity of the assessment process for some species (Lamoreux et al., 2003; Godfrey & Godley, 2008; Mrosovsky & Godfrey, 2008). These problems of data deficiency can be compounded when one considers that the IUCN state that approximately 20% of reptile species assessments have been classed as Data Deficient (IUCN, 2012).

The problem of a lack of detailed information on a particular species' status is highlighted by the increasing urgency with which some conservation actions are required, particularly for highly threatened species, with these conservation actions being pursued based on little or poor data (McGowan et al., 1998). The literature details a number of examples of misdirected conservation efforts as a result of inadequate data hampering appropriate management. For example, Seidensticker (1987) describes how two subspecies of tiger; *Panthera tigris sondaica* and *Panthera tigris virgata* became extinct as a result of inadequate

knowledge of the distribution of the last few remaining individuals, which, amongst other issues, hampered their effective conservation. Some of the *Cuora* and *Batagur* species of Asian turtles have only been known to science way beyond the point when the species has become so threatened through subsistence harvesting for the local bush meat trade, that many of the species have become ecologically non viable in the wild (Rhodin et al., 2011). Nothing was known about the Yunnan box turtle (*Cuora yuannensis*) ecology before the species was rediscovered in the pet trade in 2004 after being declared extinct in 2000 (Rhodin et al., 2011). This made the captive husbandry of a small assurance colony of the species difficult, after the subsequent discovery of a number of other individuals. However, after a decade of intensive searching, it wasn't till 2008 that the habitat supporting the species in the wild was finally found (Zhou et al., 2008; Rhodin et al., 2011). In the case of many reptiles, the most cited reason for failures within conservation translocation exercises to reduce human/wildlife conflict, is a basic lack of ecological life history data, particularly for rarer, more threatened species (Griffith et al., 1989; Dodd & Seigel, 1991). However, conservation failures and a basic lack of data hampering conservation efforts are often under reported within the literature (Smallwood et al., 1999), so many conservation management issues with regards to data deficiency go unreported.

Historically, chelonians have suffered some of the greatest population crashes of any vertebrate taxa; mostly as a result of human interventions, such as over harvesting for food, trade or habitat destruction (Rhodin et al., 2011). Between 48 and 54% of the world's chelonians are considered threatened with extinction (van Dijk et al., 2011), with this group of species at much higher risk of extinction than many other vertebrates, with amphibians considered the next most threatened (30-41%) closely followed by mammals, in particular primates (Hoffmann et al., 2010). Indeed, Madagascar supports 10% of the world's top 40 most threatened tortoises as

described by the IUCN Specialist Group for Tortoises and Freshwater Turtles (Rhodin et al., 2011). The ecology, biology and life history traits of these animals dictate that adaptation by most species of chelonian to cope with habitat alternation or any levels of harvesting is impossible on account of the longevity, low fecundity and specialised habitat requirements of many species (Bombi et al., 2011). The ease with which these slow moving, terrestrial animals can be captured by humans (Walker et al., 2004; Pedrono, 2008) and their lack of natural predators mean that populations of these *K* strategists are unable to cope ecologically with high rates of mortality within a population. This has contributed to rapid declines and even extinction among many species of tortoise within recent history with the Indian Ocean and Madagascar being focal regions for mass extinctions of tortoises (Gerlach, 2004; Pedrono, 2008; Rhodin et al., 2011). For example, the vulnerability of Malagasy chelonians can be demonstrated by the relatively well documented extinction of two species of tortoise; *Dispsochelys grandidieri* and *D. abrupta* (Raxworthy & Nussbaum, 2000; Pedrono, 2008). These two species coexisted with humans for more than 1,000 years and once occupied a large area of the central and western region of the island (Bour 1984; Pedrono, 2008). The cause of extinction, sometime before 750 years ago (Dewar, 1984) is under much debate with Raxworthy & Nussbaum (1996) having suggested that the modern day practice of regular burning of grassland and its peripheral forests, over much of the island, was responsible for destroying the original habitats of grazing animals such as giant tortoises, while MacPhee & Marx (1997) consider their extinction may be due to the human introduction of exotic pathogens that caused hyperdisease. Hunting pressure has also been speculated with remains of *D. granddidieri* displaying signs of damage through early weapons (Martin, 1966). Many of these pressures currently still persist at varying levels, threatening Madagascar's other surviving four species of endemic tortoises (Pedrono, 2008).

From an evolutionary point of view many species of tortoises have colonised remote islands and archipelagos throughout the world through rafting during the last several thousand to several million years (Caccone et al., 1999; Pedrono, 2008). This dispersal and subsequent speciation of many species of tortoises occurred on account of their ability to float and endure long periods without food or fresh water (Gerlach et al., 2006). These original colonisers have typically been left to evolve, in isolation, into the primary herbivores within these remote areas, such as the Galapagos and Indian Ocean Islands, often devoid of large terrestrial predators. However, the demise of many of these species, resulting in some cases extinction and in many cases severely impacted population sizes, began largely during the 18th century by early European seafaring explorers (Coblentz, 1978; Gerlach, 2004; Pedrono, 2008) harvesting tortoises as a protein source or unwittingly introducing non-native predatory species to these islands such as rats (*Rattus* sp.) (Thorsen et al., 2000). .

It is thought that seven species and two subspecies of tortoise have been driven to extinction by humans since approximately 1500AD, with six of these species occurring within the Indian Ocean Islands (Rhodin et al., 2011), highlighting the vulnerability of chelonians within the region. Very little is known of the rates of decline and the exact timings of subsequent extinctions of most of these species within the Indian Ocean islands (Gerlach & Canning, 1998), however all the extinct species belong to two distinct subgenera; *Cylindraspis* extirpated from the Mascarene Islands and *Dipsochelys* extirpated from Madagascar, the Seychelles and neighbouring islands (Gerlach, 2004). Casual harvesting by passing sailors and more organised harvesting operations for human consumption were probably responsible for the demise of the extinct species within the Mascarene Islands and Seychelles in particular (Gerlach, 2004).

The most detailed historical account of the demise of any of the extinct Indian Ocean Island species is for *Cylindrapis borbonica* on Reunion. This species was reported to be abundant in 1665, however by 1688 they were being heavily consumed (Gerlach, 2004) and in 1694 it was already noted that tortoises were absent from the north of the island. The most detailed historical description of the exploitation and subsequent decline of *C. borbonica* on Reunion was provided by Leguat (1709), whereby 10,000 tortoises a year were exported in the 1740s, falling to 7-8,000 in the early 1750s due to a reduction in wild populations (La Caille, 1763). In 1769 the tortoise exporting station almost closed due to a shortage of tortoises (North-Coombes, 1971), however by 1795 tortoises were considered extinct on the island (Dupont, 1969), having being wiped out through less than 200 years of human exploitation. Indeed, anthropogenic interference has played a great part in shaping the diversity of the world's chelonian species within recent history. The impact of 18th century harvesting or invasive species introductions is still being felt today by many of the remote island species that managed to survive the early collection periods, such as the Galapagos tortoises (*Chelonoidis nigra*) (Russello et al., 2005) or the ploughshare tortoise of Madagascar (*Astrochelys yniphora*) (Pedrono, 2008). The last remaining colonies of these two species in particular are still struggling to recover from population depletions inflicted centuries ago.

The use of tortoises as food, either locally as bush meat (Walker, 2010; O'Brien et al., 2003), or exported, predominantly to Asia (Nijman & Shepherd, 2007), has been a worrying conservation issue for many species within more recent times. Their use in Chinese traditional medicine (Chen et al., 2009) and capture for the international exotic pet trade (Walker et al., 2004) has also taken its toll on many species. Rarer, CITES Appendix I listed species are often the most sought after within the pet trade, causing the trade to be awash with illegal animals

(Nijman & Shepherd, 2007; Rhodin et al., 2011) and a significantly contributing factor affecting many chelonian species thought to be threatened with extinction.

Madagascar supports one of the highest rates of endemism anywhere in the world (Brooks et al., 2006) and like many other regions of high endemism Madagascar has complex patterns of micro-endemism among taxa (Goodman & Benstead, 2005; Wilmé et al., 2006). This pattern of micro-endemism holds true for Madagascar's four species of endemic tortoises, all restricted in range and thought to be facing considerable threats to their survival, through loss of habitat, collection for illegal export to support the pet trade and in some cases local consumption as food (Walker et al., 2004; Leuteritz et al., 2005; Young et al., 2008; Walker, 2010). However, unlike some of the island's more charismatic fauna, there still remains a lack of applied research into the ecology and conservation status of Madagascar's tortoises (Mittermeier et al., 2008), in particular one of the smallest genera in the world; *Pyxis* (Walker, 2009). This genus comprises two species; the flat tailed tortoise (*Pyxis planicauda*) and the spider tortoise (*Pyxis arachnoides*), both measuring less than 200mm curved carapace length (Walker et al., 2007; Pedrono, 2008) and both listed as Critically Endangered on the IUCN Red List for Threatened Species (Leuteritz & Walker, 2009; Leuteritz et al., 2009).

This study focuses on assessing the conservation status of *P. arachnoides*, a species endemic to the dry coastal forests of southwest Madagascar, occurring within approximately 10km of the coastline (Walker, 2010; Walker et al., in press). *P. arachnoides* makes an ideal model species to base a study investigating the conservation status of an ecologically poorly understood, threatened species. The species is listed as Critically Endangered on the IUCN Red List for Threatened Species (up listed from Vulnerable to Critically Endangered during a 2008 conservation status assessment), however, the criteria was met using anecdotal data or out of date

data of limited spatial resolution, based mainly on the threats of habitat loss, exploitation and subsequent population and range reduction (IUCN Red List classification criteria: A4cd+E) (Walker et al., 2007; Mittermeier et al., 2008, Leuteritz & Walker, 2009). Indeed, smaller, cryptic species from tropical regions, such as *P. arachnoides*, are often overlooked or harder to classify during conservation status assessments in comparison to larger, often mammalian species in more developed regions of the world such as Europe or North America (McKinney, 1999) which often support more available data. This current lack of published ecological, biological and real time conservation status data is hampering the conservation planning for *P. arachnoides* (Walker, 2009).

P. arachnoides was thought to have a restricted, yet continuous historical extent of occurrence within its' dry forest habitat comprising 555km of coastline (Pedrono, 2008), from the Mangoky River to Lac Anony (Bour, 1981; Pedrono, 2008) (Fig. 1). However, as a result of habitat destruction due to unsustainable subsistence agricultural practices (Seddon et al., 2000), collection for international trade and domestic consumption (Walker et al., 2004, Pedrono, 2008, Walker, 2010) the species' range is now thought to be severely reduced. The species is divided into three subspecies (Chari et al., 2005; Pedrono, 2008) (Fig. 2), with the defining morphological characteristic being the mobility of the plastron hinge. *P. a. brygooi* inhabits the coastal, dry, Mikea forest (Fig. 1a) (Walker et al., in press; Walker & Rafeliasoa, 2012), a habitat classified as a sub type of the unique southern coastal dry forests. The Mikea forests have historically stretched from the north of Toliara to approximately 30km north of Morombe (Seddon et al., 2000). Further south, *P. a. arachnoides* and *P. a. oblonga* inhabit the southern coastal dry forest (Bour, 1981; Walker et al., in press; Walker & Rafeliasoa, 2012) (Fig. 1b; 1c & 2). These arid coastal forests have long been identified as extremely important for their

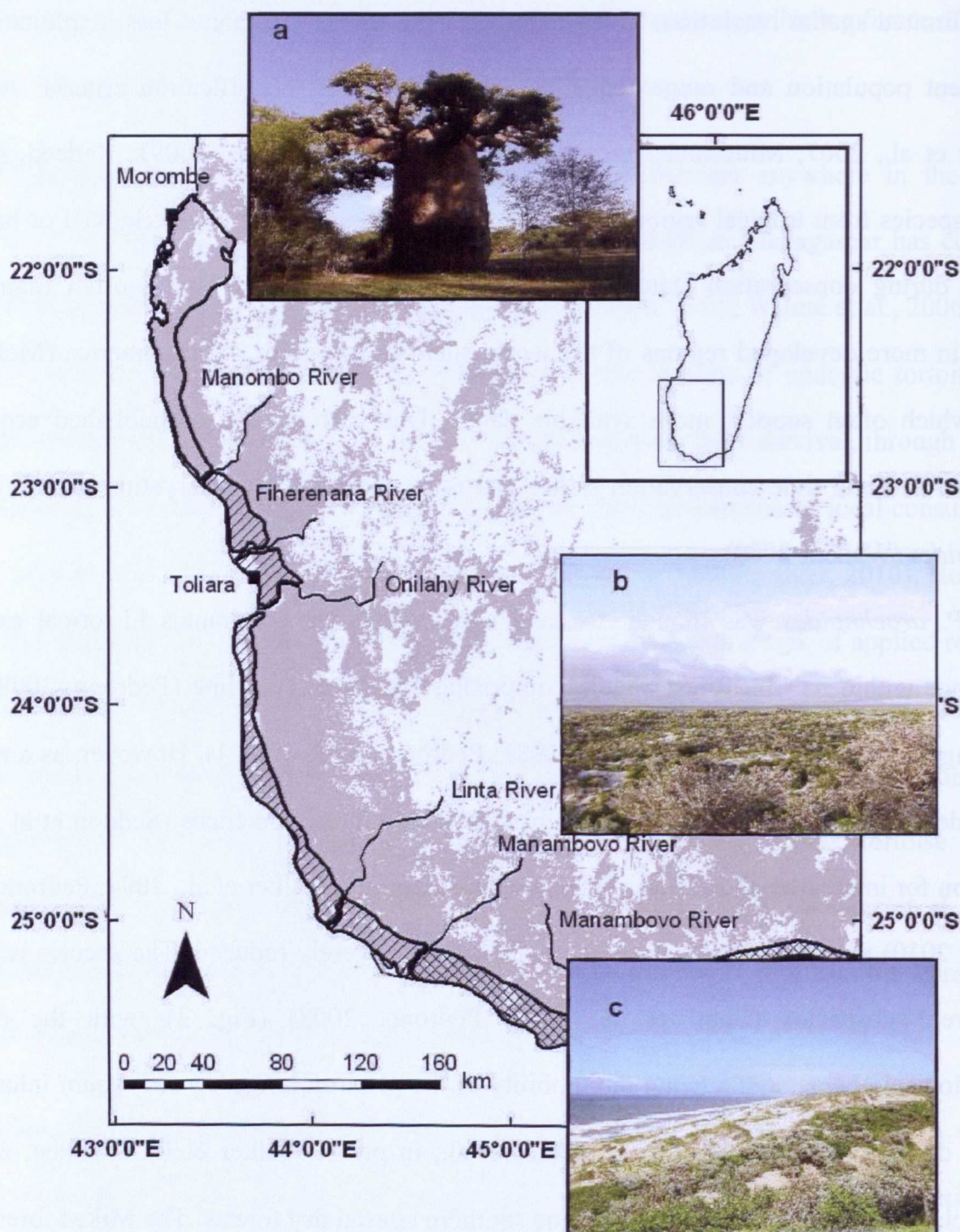


Figure 1: Suspected historical extent of occurrence of the three subspecies of spider tortoise as described by Bour, (1981) and Pedrono (2008), grey areas denote vegetation cover derived from LandSat TM7 imagery (Harper et al., 2007). Northern block (clear) denotes suspected area occupied by *P. a. brygooi*; with image of the subspecies' typically associated Mikea forest habitat (a); middle block (diagonal hatch) denotes suspected area occupied by *P. a. arachnoides* with image of typically associated dry southern forest habitat (b); southern block (cross hatch) denotes suspected area occupied by *P. a. oblonga* with the image of the typically associated coastal dune habitat/dry southern forest habitat of the extreme south. Photo credit: RCJ Walker

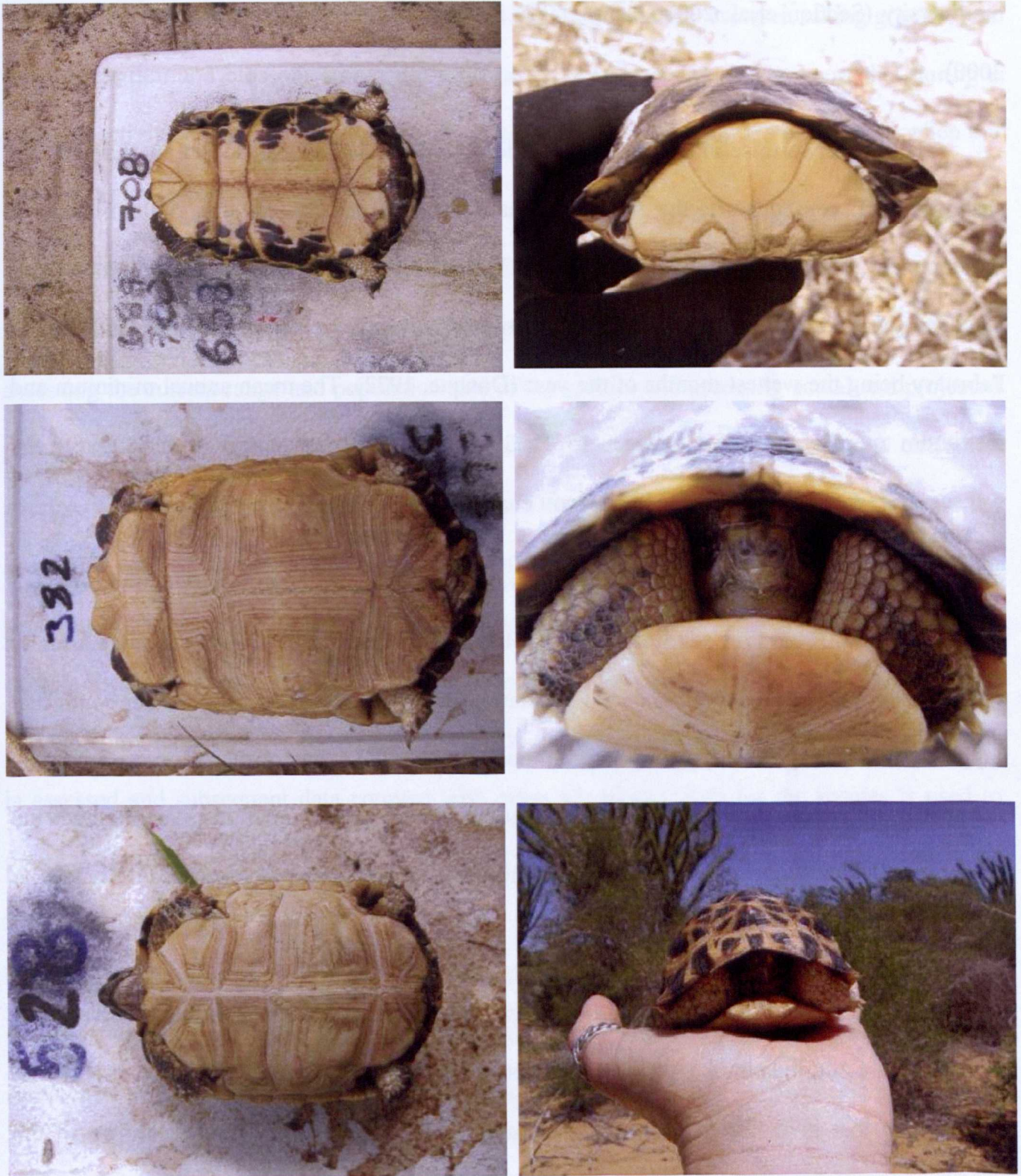


Figure 2: Typical morphology of *P. a. oblonga* showing dark plastral edge pigmentation (top left) and mobile plastral hinge allowing for full retraction of head and front legs (top right); *P. a. arachnoides* supports a semi mobile hinge (middle right and middle left) and *P. a. brygooi* typically displays a rigid plastral hinge (bottom right and bottom left). Photo credit: top left, top right, middle left, middle right, bottom left; RCJ Walker, bottom right; I Smith.

biodiversity (Seddon et al. 2000; Fenn, 2003), in particular reptiles (Raxworthy & Nussbaum, 2000).

The spider tortoise inhabits the most arid region of Madagascar due to an extreme rain shadow effect; consequently, the average annual rainfall is usually less than 500mm (Jesu & Schimmenti, 1995; Gautier & Goodman, 2003). The climate is dominated by wet and dry seasons with most precipitation occurring between November and April, with January and February being the wettest months of the year (Donque, 1972). The mean annual minimum and maximum temperature ranges between 15-21°C during the dry season and 30-33°C during the wet season respectively (Donque, 1972; Scott et al., 2006).

Vegetation communities can be highly variable throughout these forests due to differing soil types (Fenn, 2003). The sandy soils of the Mikea forest, within *P. a. brygooi*'s range, usually support taller and more densely situated vegetation than the calcareous soils further south that support dwarf tree species, typically 3-6m in height within the range of the two more southerly sub species of tortoise (Lowry et al., 1997). Plant families characteristic of this region include the xerophytic Didiereaceae and Euphorbiaceae and the baobabs of the Bombacaceae (Gautier & Goodman, 2003).

Despite inhabiting a highly seasonal environment *P. arachnoides* exhibits little variation in habitat use throughout the year (Walker et al., 2012a). However, Walker et al. (2012a) demonstrate that juveniles favour areas of denser canopy cover. Very little is known of the foraging habits and diet of this species (Walker et al., 2007) and even less is known about the reproduction and life history traits of this species within the wild. Glaw & Vences (1994) reported that the species' diet includes young leaves and cow dung containing insect larvae.

Casual field observations suggest that the species is an opportunistic browser, taking grasses, low level vegetation and blossom during the wet season. Walker et al. (2007) report that during a seasonal activity study, individuals were never recorded feeding during the dry season, when the animals typically enter an aestivation phase.

This study aims to establish if, indeed, the current conservation status of *P. arachnoides* fulfills the criteria for the assigned IUCN Red List Critically Endangered status, through assessing the current range and population size of the species and assessing actual and projected population declines using accepted methods suitable for small, cryptic, dry forest chelonian species. A range wide presence/absence survey across the suspected extent of occurrence for the species is applied, to assess the current area of occupancy, followed by a distance sampling procedure (Thomas et al., 2010) to assess current population size and density. Finally, through capture-mark-recapture (CMR) analysis (White & Burnham, 1999), the mean annual survivorship of a population of tortoises within the core of the species range (Walker et al., 2007) is assessed and subsequent data coupled with other life history data for the species is used to develop a population matrix model (Lefkovich, 1965; Caswell, 2001), in an effort to quantify the extinction risk to a spider tortoise population as a result of anthropogenic habitat deterioration. Conversely, the results of this study focusing on this one model species, will assess the suitability for the potential to apply these techniques across the taxon and the plethora of poorly researched, yet potentially highly threatened chelonian species.

Chapter 2: Conservation of the Madagascar Spider Tortoise (*Pyxis arachnoides*) amid changing land use policy: Assessing the spatial coincidence of relict populations within protected areas and mining concessions^{3,4}

Introduction

Geographical range size and how it changes through time is one of the fundamental ecological characteristics of a species (Gaston, 2003). However measurement of geographical range is not straightforward (Gaston, 1991, 1994, 2003) and from a historical perspective, a multitude of measurements were often used to assess the range of species. For example, vertebrate biologists have used the known extent of a species' habitat to predict its presence or absence in an area (Baker, 1956; Armstrong, 1972). From a current conservation perspective, it is now widely regarded that geographical range can be distinguished through two different kinds of measure; 'extent of occurrence', which captures the overall geographic spread of the localities at which a species occurs and 'area of occupancy' which typically is much smaller and is defined by the area of distributions where the species can be actually found, determined from range wide occurrences (Gaston & Fuller, 2009).

³ Walker, R.C.J., Gardner, J.C., Rafeliasoa, T.H., Smith, I & Razafimanatsoa, R. (in press) Conservation of the Madagascar Spider Tortoise (*Pyxis arachnoides*) amid changing land use policy: Assessing the spatial coincidence of relict populations with protected areas and mining concessions. In *Turtles on the Brink in Madagascar; Proceedings of Two Workshops on Status and Conservation of Malagasy Tortoises and Freshwater Turtles* (eds Castellano, C.M., Randriamahazo, H., Lewis, R.E., Mittermeier, R.A., Hudson, R. & Rhodin, A.G.J.). Chelonian Research Monographs, Lunenburg, MA, U.S.A.

⁴ Walker, R.C.J. (2010) The decline of the northern Madagascar spider tortoise (*Pyxis arachnoides brygooi*). *Herpetologica*, 6, 411-417. - Appendix 1

The range size of narrowly distributed species plays a key role in categorising species according to their short term likelihood of extinction (Gaston & Fuller, 2009). Therefore in an increasingly human dominated natural environment, the management of such species needs to include not only information on the current spatial distribution of the species in question (Gaston, 2003; Gaston & Fuller, 2009), but also the potential or actual land use and land tenancy, within this current range, which may potentially have future negative impacts on the species' distribution (Scott et al., 1993). *P. arachnoides* is one such species which is through to display vulnerability due to restricted range (Pedrono, 2008; Walker, 2010). Moreover, this lack of available data describing the range is intern hampering conservation initiatives for this Critically Endangered species (Mittermeier et al., 2008).

To date, the extent of occurrence of *P. arachnoides* has largely be based on the range of the species' dry coastal forest habitat, with a very limited application of tortoise presence/absence field data (Bour, 1981; Pedrono, 2008). These authors state that the northern subspecies of spider tortoise; *P. a. brygooi* inhabits the coastal, dry Mikea forest (Fig. 1; see Chapter 1), a habitat classified as a sub type of the southern dry spiny forests; historically stretching from the north of Toliara to approximately 30 km north of Morombe (Seddon et al., 2000; Fig. 1). *P. a. brygooi* is thought to occupy a zone of forest spanning approximately 102 km of coastline between the Manombo River and the forests north of Morombe (Pedrono, 2008) (Fig. 1). Further south, *P. a. arachnoides* and *P. a. oblonga* are thought to inhabit approximately 258 km and 195 km of coastline respectively (Pedrono, 2008) (Fig 1) within the southern dry spiny forest complex (Fenn 2003). However, Pedrono (2008) acknowledges that these are probably largely area of historical extent of occurrence and the range of the species is likely fragmented as a result of habitat loss from small scale, unsustainable agricultural practices

(Gardner, 2011), tortoise collection to support the exotic pet trade (Walker et al., 2004) and to some extent collection as local bush meat by the Mikea tribe (Walker, 2010).

In addition to this, two major developments in land use and governance have occurred within the range of *P. arachnoides* over the last decade; the expansion of the protected area system (Système d'Aires Protégées de Madagascar; SAPM), and the liberalisation of the mining sector. As a result of a pledge made at the Vth World Parks Congress in Durban in 2003, Madagascar's government will increase the country's protected area coverage threefold by 2012 (Rabearivony et al., 2010). A number of new protected areas have, or are currently being established within the dry coastal forest ecoregion of the southwest, which was previously the least represented ecoregion within the protected area network (Fenn, 2003; Gardner, 2011) and is suffering the fastest rates of forest loss in the country (Harper et al., 2007).

In an effort to improve the scant ecological knowledge of this threatened species and to further improve conservation management planning, the work reported within this chapter applies a detailed presence/absence survey across the extent of occurrence of *P. arachnoides*, described by Bour (1981) and Pedrono (2008). This survey establishes a real time distribution Geographical Information System (GIS) detailing the area of occupancy for the species (Gaston & Fuller, 2009). These data are then applied, in conjunction with further spatial distribution layers (Gustafson et al., 2001; Anadón et al., 2006) comprising the proposed or existing protected area distribution and the land proposed for mineral extraction to this GIS. These data then assess the potential conservation risk to the species resulting from mineral exploitation across the current area of occupancy.

Methods

The maps published by Bour (1981) and Pedrono (2008) detailing the extent of occurrence of *P. arachnoides* were scanned from original documents and converted in to electronic Joint Photographic Experts Group (JPEG) files. These JPEGs were imported into the GIS software ArcMap (ArcGIS 9.0), georeferenced and then polygons representing the extent of occurrence of the species were produced using the digitizing function. Using a base map of southern Madagascar these polygons were used as the base layer for our GIS database. Shapefiles derived from high-resolution remotely sensed imagery (IKONOS and QuickBird) from Google EarthTM (Fig. 3) and shapefiles representing southern dry spiny forest classification derived from Landsat Enhanced Thematic Mapper Plus (ETM+), acquired from Conservation International and used in the production of the GIS reported in Harper et al., (2007) were imported into this studies' GIS. The Landsat shapefiles represent a supervised classification based on a simple set of classes: forest or non-forest using Erdas imagine 8.4. software (Harper et al., 2007).

Unlike *Astrochelys radiata*; a tortoise species sympatric in part of its range with *P. arachnoides*, spider tortoises are seldom found in degraded habitats, such as areas cleared for charcoal production or agriculture plantations (Pedrono, 2008; Walker et al., 2012a; Fig. 3). Therefore, using the polygon describing the extent of occurrences (Bour, 1981; Pedrono, 2008) as a geographical guide, the entirety of the extent of occurrence of *P. arachnoides* plus some areas of suitable habitat within the periphery of the range were categorised into the following two classes; suitable habitat (intact forest) and non suitable habitat (degraded forest or areas of cleared forest). The high degree of resolution of Google EarthTM images (4m pixel resolution) allowed for the classification to be undertaken by human eye (Ustun et al., 2004) (Fig. 3). This classification revealed 69 suitable survey areas (Fig. 3; 4). All spatial data were georeferenced and both polygon data and the GIS database were projected to WGS84.

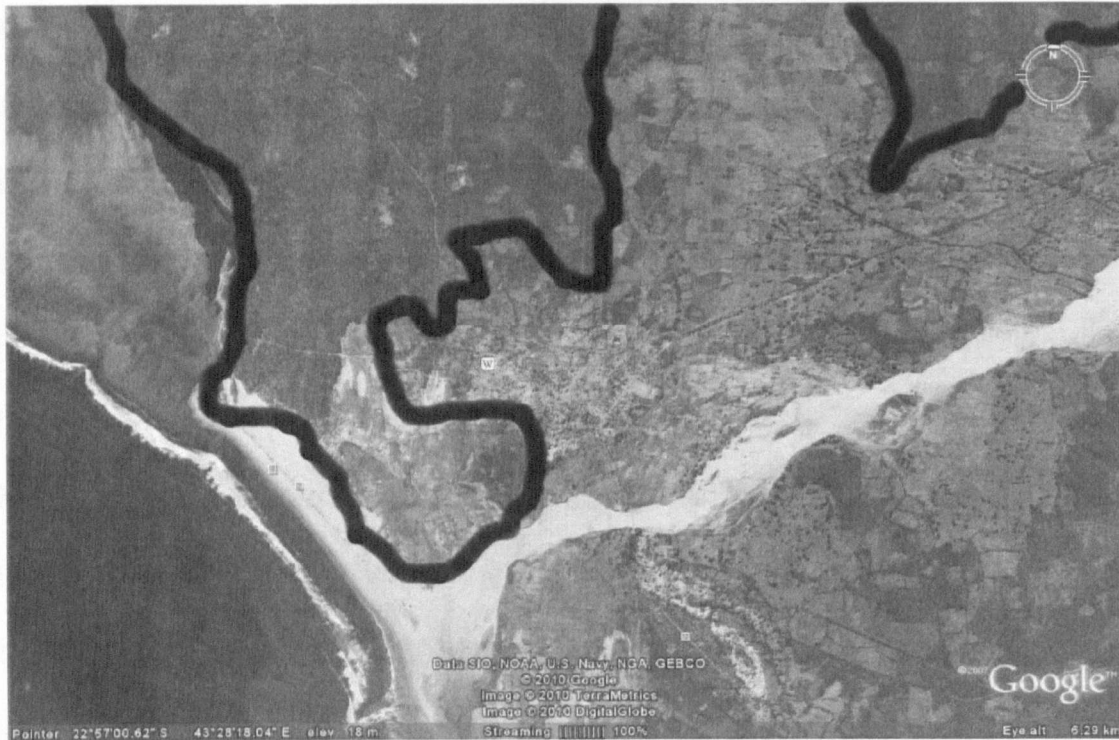


Figure 3: Google Earth image of a section of the survey area within the Manombo River discharge point, southwest coastal Madagascar. The dark line delineates an area of classified intact habitat to the north of the line that was selected for surveying, with degraded classified land south of the line characterized by parcels of agriculture land and livestock corrals. These high resolution images were also used in conjunction with the Landsat imagery to identify the limits of the polygon boundaries for parcels of habitat that support tortoise populations and to identify areas of degraded habitat and areas devoid of tortoises.

Across these 69 survey areas, a total of 131 1-km transects were surveyed (Fig. 4) and concurrent to each transect a timed search was also undertaken (Walker, 2012). Transect and timed search sites were allocated to as many areas as were physically accessible within the wider 69 survey areas, with field work undertaken during the logistically challenging wet season. Field work was undertaken during January and February 2009, 2010, and 2011 during the annual period of heightened tortoise activity (Walker, 2012; Walker et al., 2012a) Surveying was limited to between 0630h–1030h and 1530h–1830h during the cooler parts of the day, when these crepuscular tortoises are most active (Walker, 2012; see Chapter 3).

Upon reaching each survey point, two observers traversed each transect, taking an easterly bearing for 1km using the tracking function on a hand held GPS to measure distance. The surveyors walked side by side, each carefully searching for tortoises on their respective side of the transect line and directly in front of them. Surveyors moved very slowly, with transects taking on average $77.3 (\pm 40.2)$ minutes to traverse, with the time being dependent upon terrain and density of the vegetation. Spider tortoises do not spend time under the ground in burrows, unlike some species of desert tortoises such as *Gopherus* spp. (McCoy et al., 2002), thus ensuring easier detection, however the species can often be partially buried in the substrate. Because of their small size and cryptic nature (Walker et al., 2007; Walker, 2012) tortoises were normally detected only within 3m of the middle of the transect line. As a result, an additional two surveyors undertook a timed search concurrently to the transect survey. Each timed search lasted the length of the time taken to traverse the transect with surveyors searching at least 10m from the middle of the transect to eliminate duplicate detection by the two teams. Timed searchers focused their search on the base of low lying vegetation, a micro habitat favoured by the species (Walker et al., 2007; Pedrono, 2008). Walker (2012) has shown that in field trials, adult spider tortoises during the summer months support a detection probability of 1.0 (see Chapter 3). Detected tortoises were marked using a small dot of nail polish on the top of the carapace to avoid duplicate counting.

Data Analysis

Establishing population distribution

The reliance of spider tortoises upon intact habitat (Walker et al., 2012a), suggest that the species will generally not move across large open degraded areas. Waypoints marking the start of each

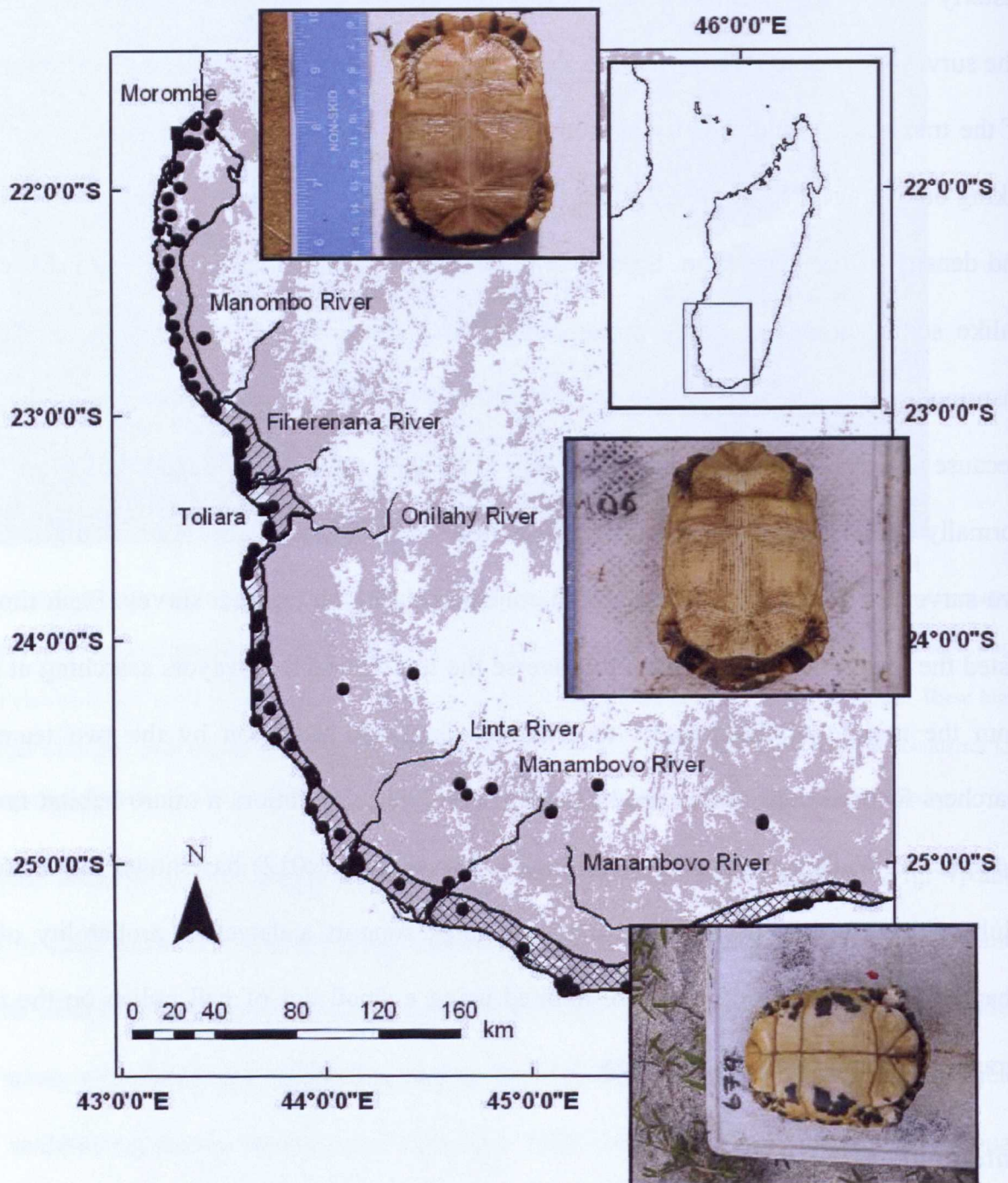


Figure 4: Suspected historical extent of occurrence for the three subspecies of spider tortoise described by Bour, (1981) and Pedrono (2008), with *P. a. brygooi* to the north, *P. a. arachnoides* to the middle of the range and *P. a. oblonga* to the south of the range with corresponding photos illustrating the varying plastron morphologies (Chapter 1). Vegetation cover layer is represented in grey and 131 field survey points are overlaid into the GIS. Photo Credits: RCJ Walker

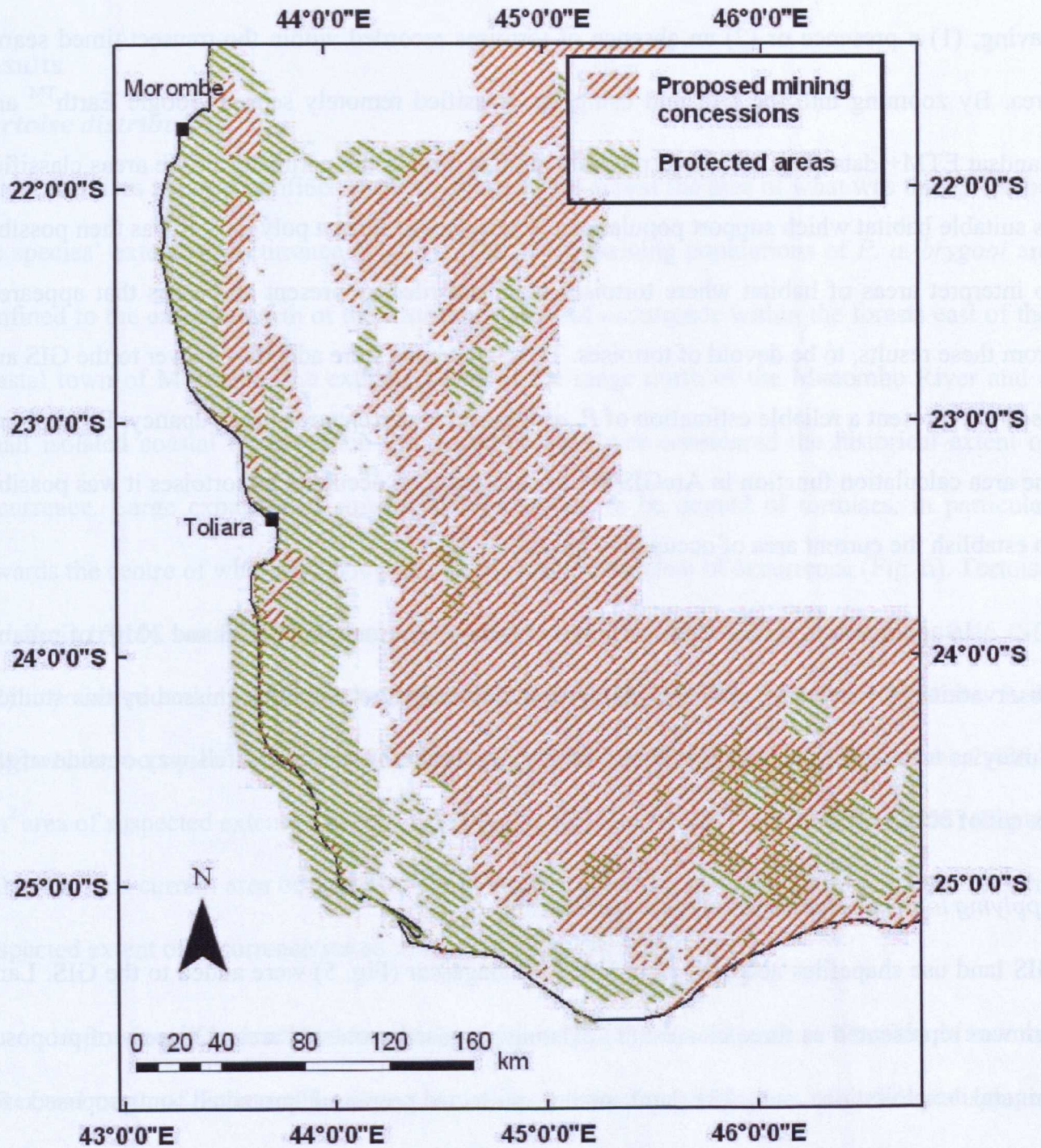


Figure 5: Spatial distribution of existing or proposed protected areas under the Madagascar Protected areas expansion program (green cross hatch) and sites proposed under the Madagascar Mining Code for mineral extraction (red cross hatch) within southwest Madagascar.

transect and timed search were added to our GIS (Fig. 4) and each waypoint was coded as either having; (1) a presence or (2) an absence of tortoises recorded within the transect/timed search area. By zooming into the GIS and using the classified remotely sensed Google Earth™ and Landsat ETM+ data (Fig. 3), it was possible digitize around the perimeter of the areas classified as suitable habitat which support populations of tortoises to form a polygon. It was then possible to interpret areas of habitat where tortoises were recorded as present and areas that appeared, from these results, to be devoid of tortoises. These polygons were added as a layer to the GIS and used to represent a reliable estimation of *P. arachnoides*' current area of occupancy. By applying the area calculation function in ArcGIS 9.1 to each polygon occupied by tortoises it was possible to establish the current area of occupancy in km².

In addition to the field data, two recent reports were included (2008 and 2010) of reliable observations of very small remnant populations. These areas were either missed by this studies' survey as a result of the very small size of the population or the record fell way outside of the extent of occurrence.

Applying land use classes to tortoise distribution

GIS land use shapefiles acquired from WWF Madagascar (Fig. 5) were added to the GIS. Land use was represented as three classes: (1) existing/proposed protected area; (2) areas of proposed mineral exploitation; and, (3) land neither protected/proposed protected or proposed for exploitation. The data layer representing the current range of the tortoises was then overlaid on the land use data layer, and polygons were created through manual digitizing to create three classes within the tortoise' range; (1a) range within proposed protected areas; (2a) range within

proposed exploitation areas; and, (3a) range within neither protected nor exploited. The area calculation function was then applied to these three classes.

Results

Tortoise distribution

Spider tortoises are now confined to eight isolated sites across the area of what was thought to be the species' extent of occurrence (Fig. 6). The last remaining populations of *P. a. brygooi* are confined to the extreme north of the historical extent of occurrence within the forests east of the coastal town of Morombe, the extreme south of the range north of the Manombo River and a small isolated coastal forest within the centre of what was considered the historical extent of occurrence. Large expanses of suitable habitat appear to be devoid of tortoises, in particular towards the centre of what was thought to be the historical extent of occurrence (Fig. 6). Tortoise density is highly variable, with a mean encounter rate of 1.7 (SD 6.2), ranging from 0-46 (SD 6.2) tortoises recorded per linear km of transect for the region surveyed north of Toliara. *P. a. brygooi* now occupies a total area of occupancy of 499.6 km² (Fig. 6), compared to the 2,438.8 km² area of suspected extent of occurrence described by Bour (1981) and Pedrono (2008) (Fig. 6; Table 1). This current area of occupancy represents a reduction of 1,939.2 km² (79.5%) from the suspected extent of occurrence stated in the previous studies (Table 1).

A previously undescribed transitional zone within the coastal zone south of the Manombo River and north of Toliara (Fig. 6) was discovered, whereby populations of tortoises displayed variable morphology. Individual tortoises in this zone display three distinctly different variations in plastron hinge mobility morphology. Some individuals display characteristics consistent with *P. a. brygooi*, some animals display characteristics consistent with the common subspecies *P. a. arachnoides* and there are tortoises with morphological traits displaying

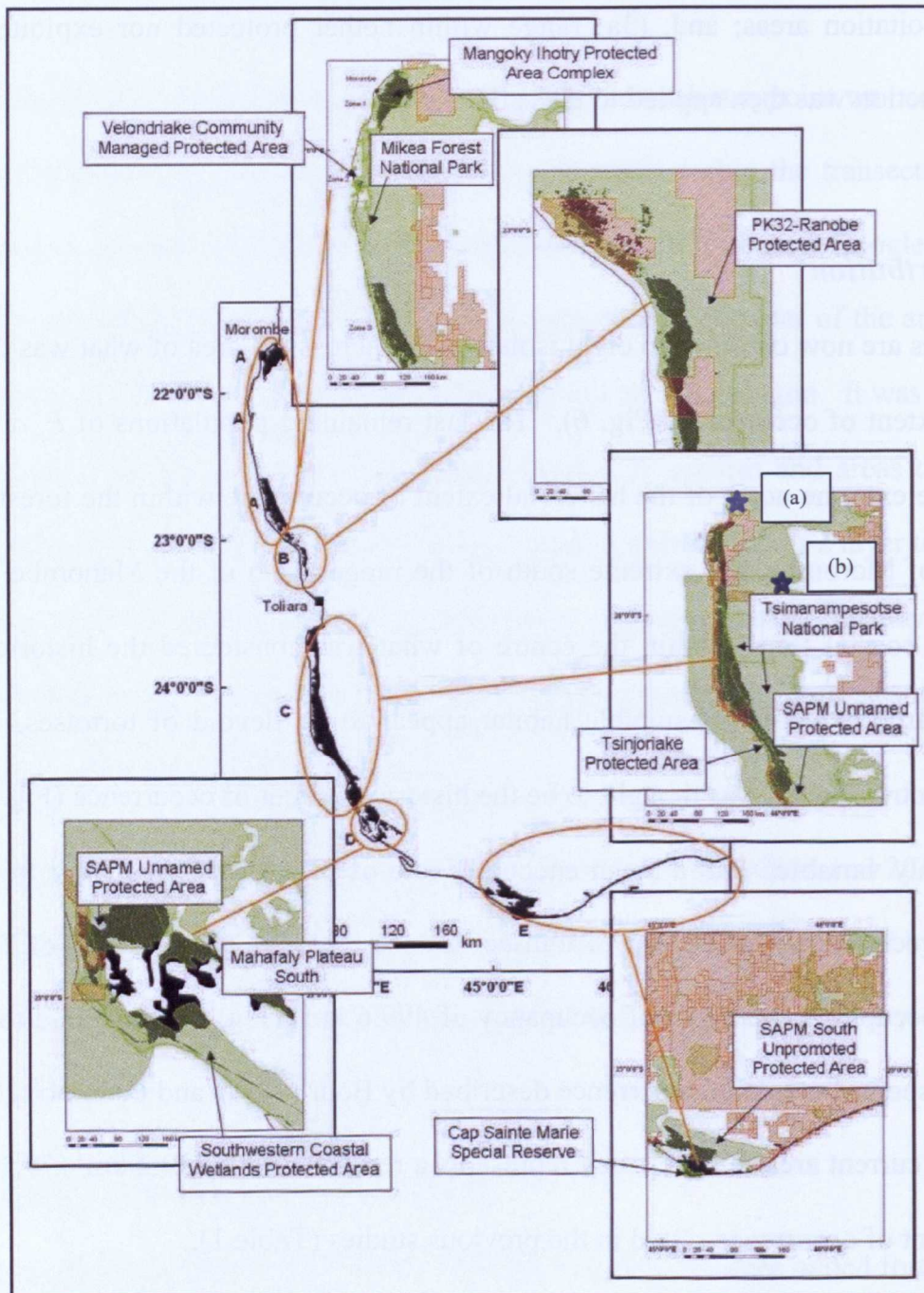


Figure 6: Current area of occupancy of the three subspecies and two intergrade populations of spider tortoise displayed in black (central map); A=*P. a. brygooi*; B= *P. a. brygooi*/*P. a. arachnoides* intergrade population; C=*P. a. arachnoides*; D= *P. a. arachnoides*/*P. a. oblonga* intergrade population; E = *P. a. oblonga*. Blow out maps represent corresponding populations in relation to the proposed/existing protected areas displayed in green cross hatch and areas of proposed mineral extraction displayed in red cross hatch. (a) The point represented by the star to the north of *P. a. arachnoides*' area of occupancy represents the remnant population missed by the survey, reported by (Scott et al. 2008). (b) The star to the east of *P. a. arachnoides*' area of occupancy represents the individual tortoise missed by the survey, reported by Rick Hudson (Pers. comm.).

a mixture of the two subspecies. It is suggested that this area is a zone of intergradation between *P. a. brygooi* and *P. a. arachnoides*. This population of intergrades covers an area of occupancy measuring 99.7 km² (Fig. 6; Table 1) and falls within the zone previously described by Pedrono (2008) and Bour (1981) as part of *P. a. arachnoides* 'suspected extent of occurrence' (Fig. 4).

Spider tortoises appear to be largely absent within the coastal zone between the Fiherenana and Onilahy Rivers (Fig. 6), probably as a result of poaching and habitat loss on account of its close proximity to the provincial capital; Toliara (Walker & Rafeliasoa, 2010). However a very small isolated population was recently reported to occur approximately 8km north of the Onilahy River (Scott et al., 2008) (Fig. 6). An unfragmented zone supporting a large population of *P. a. arachnoides* begins south of the Onilahy River (Fig. 6). This population stretches south along the coastline for approximately 72km (Fig. 6). One isolated individual female tortoise was found during a separate study in March 2010, 62 km inland on the main road serving the coastal region south of the Onilahy River (Rick Hudson, pers. comm.) (Fig. 6). On account of the large discrepancy in what is considered to be the species natural range, and that it was found next to the only route in or out of the region, it is suspected that this tortoise was a probable escapee that had fallen off an ox cart used by a poaching operation.

A further undescribed zone of intergradation between *P. a. arachnoides* and *P. a. oblonga* occurs either side of the Linta River, occupying an area of 267.0 km (Fig. 6; Table 1), in what was historically considered to be the range of *P. a. arachnoides* (Bour, 1981; Pedrono, 2008) (Fig. 4).

Tortoise density for *P. a. arachnoides* and the population of *P. a. arachnoides*/*P. a. oblonga* intergrades is less variable than that of *P. a. brygooi* and the northern intergrade

Table 1: Current area of occupancy displayed against the suspected historical extent of occurrence documented by Bour (1981) and Pedrono (2008)[†], in addition to the extent of these ranges for each population of tortoise that fall within existing or proposed protected areas or sites of proposed mineral extraction.

Subspecies	Current area of occupancy (AOO) (km ²)	Historical extent of occurrence (EOO) [†] (km ²)	Reduction from EOO-AOO (km ²)	% reduction from EOO-AOO	Current AOO in Protected Areas (km ²)	% of current AOO in Protected Areas	Current AOO in proposed extraction areas (km ²)	% current AOO in proposed extraction areas	Protected areas	Proposed resource to be extracted	No. of potential extraction sites
<i>P. a. brygooi</i>	499.59	2438.76	1939.17	79.51	499.59	100.00	0.00	0.00	Zone 1 - Mikea Forest National Park, Mangoky Ihotry Protected Area Complex,	N/A	0
									Zone 2 –Velondriake Community Managed Protected Area		
									Zone 3 Mikea Forest National Park		
<i>P. a. brygooi</i> / <i>P. a. arachnoides</i> intergrade	99.71	-	-	-	55.10	55.26	37.80	37.91	PK32-Ranobe Protected Area	Zircon, Ilmenite	2
									Tsimanampesotse National Park Extension, Tsimanampesotse National Park, Tsinjoriake Protected Area, SAPM Unnamed/Unpromoted Protected Area		
<i>P. a. arachnoides</i>	1029.09	3177.70	2148.62	67.62	795.50	77.30	205.47	19.97		Calcaire, Ilménite, Monazite, Zircon, Granite	26
<i>P. a. arachnoides</i> / <i>P. a. oblonga</i> intergrade	266.97	-	-	-	186.48	69.85	10.66	3.99	Southwestern Coastal Wetlands Protected Area, Mahafaly Plateau South, Unnamed/Unpromoted Protected Area	Ilménite, Granite, Calcaire, Zircon	3
<i>P. a. oblonga</i>	568.45	2865.48	2297.03	80.16	268.00	47.15	196.94	24.64	Cap Sainte Marie Special Reserve, SAPM South Unpromoted Protected Area	Ilménite, Zircon	1
Total	2463.81	8481.94	6018.13	70.75	1804.67	73.52	450.87	18.30			32

population. A mean encounter rate of 2.3 (SD \pm 2.2) tortoises, ranging from 0-7 (SD \pm 2.2) tortoises per linear km of transect was recorded. *P. a. arachnoides* now occupies a total area of occupancy of 1,029.1 km² (Fig. 6; Table 1), compared to the 3,177.7 km² area of suspected extent of occurrence described by Bour (1981) and Pedrono (2008) (Fig. 4; Table 1). This area of occupancy represents a reduction of 2,148.6 km² (67.6%). However, comparing a species' extent of occurrence with area of occupancy must be undertaken with caution on account of both being considered two different ecological classification schemes and not directly comparable. Moreover, it should be noted that the reclassification of the range of the subspecies to include the two populations of intergrades significantly contributes to the decrease in range of *P. a. arachnoides*. The area of occupancy of *P. a. oblonga* equates to 568.5 km² of forests around the Cap Sainte Marie region and the dunes stretching east of the Cape (Fig. 6, Table 1); only covering some 19.8% of the extent of occurrence described by Bour (1981) and Pedrono (2008).

Land use analysis

With the proposed protected area expansion in place all 499.6 km² of *P. a. brygooi*'s current area of occupancy falls within three newly proposed protected areas (Fig 6; Table 1) and currently no proposed mineral extraction is planned for any of this subspecies' remaining range. The northern reaches of the most northerly population of *P. a. brygooi* falls within the Mangoky/Ihotry Protected Area Complex, and the southern portion of this population falls within the Mikea Forest National Park (Zone 1; Fig. 6; Table 1). The small population to the middle of the historical range is covered by the Velondriake Community Managed Marine and Coastal Protected Area (Zone 2; Fig 6; Table 1).

The *P. a. brygooi/arachnoides* intergrade population south of the Manombo River faces the greatest potential impact from proposed mineral extraction, with a possible 37.9% of the remaining area of occupancy under threat. Our results suggest that 55.3% of this population falls within protected areas (Fig. 6; Table 1). *P. a. arachnoides* currently covers the greatest remaining area of occupancy, of all the subspecies or intergrade populations. This group covers a continuous coastal belt of forest measuring 1,029.1 km². Fragments of this population occur within four protected areas, including one area which has been prioritised for inclusion in the protected area network, but is currently unprotected (Fig. 6, Table 1). *P. a. arachnoides* is also potentially threatened by 26 mineral extraction operations (Table 1).

The only protected part of *P. a. oblonga*'s narrow range is within Cap Sainte Marie Special Reserve (Fig. 6). However, some of the range falls within a currently unpromoted proposed protected area. Of the remaining range only 268 km² is currently within this one protected area and the one proposed area (Table 1, Fig. 6), and represents the smallest protected population of the three described subspecies.

Discussion

Pedrono (2008) stated that authors as far back as the late 1970s were reporting suspected declines of *P. arachnoides* populations. Bour (1981) suggested that although the spider tortoise's potential range is relatively large (i.e. extent of occurrence), populations may be fragmented and contain variable numbers of individuals. Raxworthy & Nussbaum (2000) estimated there are probably more than 10 populations of *P. arachnoides*, thus recognizing that the population was probably fragmented to some degree and the suspected extent of occurrence was probably not accurate. However, until now no field data were available to quantify this fragmentation for any of the three subspecies. The perceived decline of a 70.8% reduction in range when one compares

the current area of occupancy compared to the extent of occurrence described by Bour (1981) and Pedrono (2008) appears dramatic. However, the earlier estimates of range were made by ground truthing only 28 sites (Bour, 1981) without any GIS analysis and when one considers that the most of the loss in range has been around the extremities of the species range if one was to compare the historical extent of occurrence against the current extent of occurrence the perceived loss would be much less. This study involved far greater ground truthing and spatial analysis effort and as a result the distribution estimate for the species is spatially better resolved, so that discontinuities and disjunctions within the range are more apparent (Gaston, 1994; Goehring et al., 2007). Despite this, habitat loss and poaching has, and continues to have, serious impacts on the species' distribution, with range decline often a strong predictor of extinction risk (Gaston & Fuller, 2009). For example, Walker et al. (2012c) reports projection modelling exercises that show that a population of spider tortoises within the Anakao region is declining by 1.4% year⁻¹ as a result of habitat loss (see chapter 5). Also tortoises have all but been extirpated from most regions where the local populous hunt them for food particularly within the north of the range (Walker, 2010; Fig. 6) in the regions sympatric with the Mikea tribe. As a result of the previously speculative approach to distribution mapping by Bour (1981) and Pedrono (2008) the true rate of decline in range is relatively unknown for the species. However, these data presented here should now be used as a baseline for future distribution monitoring of area of occupancy.

False absences are always considered a risk when undertaken presence/absence surveys using single visit surveys. The precision of this survey could possibly have been improved through undertaking site occupancy modelling (Mackenzie et al., 2002), however this methodology would have required multiple visits to each survey site, which would have been

logistically unfeasible. Moreover, site occupancy modelling becomes more relevant for species with a detection probability of <1 .

The results of this study show that *P. a. brygooi* is confined to three isolated areas of forest across its historical suspected extent of occurrence. Habitat destruction and fragmentation has had, and could continue to have, wide-ranging impacts for the conservation of this subspecies. Aponte et al. (2003) have demonstrated that habitat fragmentation amongst forest tortoises (in this case *Chelonoidis carbonaria*) can result in altered age structure and population density. *P. a. arachnoides* enjoys a relatively uninterrupted area of occurrence (Fig. 6). However this region of coastline is relatively heavily populated compared to the Mikea forests further north and is suffering from habitat loss and invasion from non native floral species such as *Opuntia* spp. (Walker & Rafeliarsoa, 2010). In addition to range reduction as a result of habitat fragmentation, the spider tortoise could be currently facing direct exploitation from the pet trade. During the past 20 years very heavy levels of collection took place prior to the species becoming listed on Appendix I of the Convention on International Trade in Endangered Species (CITES) in 2004 (Walker et al., 2004; Pedrono, 2008). This harvesting may still pose a problem for the species, with a confiscation of 150 spider tortoises made by Malagasy authorities in March 2012 (Walker pers. comm.).

Seventy three and a half per cent of the remaining range of spider tortoises lies within recently gazetted or existing protected areas, including 100% of the *P. a. brygooi* population. Four of these areas across the species range, however, whilst prioritised for protected area creation within SAPM, are yet to attract promoters to catalyse the protected area establishment process. With the exception of the two National Parks (Mikea Forest and Tsimanampesotse) and Cap Sainte Marie Special Reserve, all proposed new protected areas in the region are gazetted as

IUCN category III, V or VI multiple-use PAs, which will be co-managed by local community associations (Gardner, 2011). Outside such protected areas, a significant proportion of the remaining global population of spider tortoises could potentially face threats from future mineral extraction under the proposed mining schemes for the southwest. Currently, 18.3% (450.9 km²) (Table 1) of the range of the species' falls within proposed mineral extraction sites. As a result, c. 40% of the range of the northern intergrade population (Table 1) currently occurs within sites proposed for mineral extraction, with a need for some sort of adaptive conservation management or mitigation to be adopted by the mineral extraction companies in collaboration with, or under the guidance of, local conservation practitioners or NGOs.

This new regional protected area structure could facilitate the implementation of large scale community sensitization programs, such as the environmental education, community outreach work and tortoise poaching enforcement work currently being undertaken on a smaller scale by WWF (WWF, 2010). Communities can also be encouraged to address tortoise hunting for bush meat in the Mikea region through the introduction of local bylaws (*dina*) banning the harvest of tortoises, although the success of this approach is dependent on community buy-in and the perceived legitimacy of such rules (Rabesahala Horning, 2003; Andriamalala & Gardner, 2010). It is suspected that most of the poaching of tortoises for the pet trade is undertaken by gangs from outside of the region and will therefore be more difficult to address (WWF, 2010). However WWF has had a limited amount of success in intercepting poaching gangs and poached tortoises in the region (WWF, 2010). The conservation issues facing these last remaining populations of spider tortoises are wide ranging and complex, and protected area creation alone will not be sufficient to guarantee their viability. However, the fact that most areas that support

tortoises are now managed in some way will make a more coordinated response to their conservation easier to implement.

Chapter 3: Global population estimate of the Critically Endangered Madagascar spider tortoise (*Pyxis arachnoides*)⁵⁶

Introduction

Estimating abundance or density of a population of a particular species is important for developing sound conservation policy and management protocols (Buckland et al., 2005; Thomas et al., 2010), with these data becoming particularly important for threatened or endangered species (Swann et al., 2002; Smolensky & Fitzgerald, 2010). Despite the considerable interest in the amphibian and reptile faunas of Madagascar and the widely held view that the island represents one of the world's top conservation priorities (Myers et al., 2000), very little is known about the actual population status of many of these species (Raxworthy & Nussbaum, 2000).

Almost nothing is known of the current population status of the spider tortoise *Pyxis arachnoides* and as a result effective conservation of the species is thought to be compromised (Mittermeier et al., 2008; Walker, 2009). To date the population size of *P. arachnoides* has only been speculated or been based upon data from a very narrow geographical region within the species range. For example, Pedrono (2008) claimed an approximate figure of 2-3 million animals, while Randriamahazo et al (2007) suggested a figure of 282,000. Randriamahazo et al.'s (2007) estimate was based on data from one isolated area (Cap Sainte Marie Special

⁵ Walker, R.C.J & Rafeliasoa, T. H. (2012) Status of the relict population of the Critically Endangered Madagascar spider tortoise *Pyxis arachnoides*. *Oryx*. 46, 457-463. – Appendix 1

⁶ Walker, R.C.J. (2012) A critical evaluation of field survey methods for establishing the range of a small, cryptic tortoise: (*Pyxis arachnoides*). *Herpetological Journal*. 22, 7-12. – Appendix 1

Reserve), using incidental sightings of *P. a. oblonga* recorded by Luteritiz et al., (2005) during their wider study focusing on *A. radiata*. Currently the species is distributed across eight fragmented populations encompassing an area of occupancy totalling 2,464 km² (Walker et al., in press; see Chapter 2) of coastal dry forest, with a recent loss in range that has thought to have come about largely as a result of anthropogenic drivers (Walker et al., 2012c; see Chapter 1).

Line transect distance sampling is a widely used technique for estimating the density and/or abundance of biological populations (Thomas et al., 2010) and is considered particularly effective for establishing population estimates for tortoises (Swann et al., 2002; Anderson et al., 2001; Young et al., 2008). However, to produce an unbiased density estimate using distance sampling there are a number of assumptions that must be met in the survey design and data collection (Buckland et al., 2001; Thomas et al., 2010). The most important assumption is that animals on or near the centre of the line transect are always detected (i.e. detection probability at zero distance; $g(0)=1$). This can be problematic when surveying cryptic species such as *P. arachnoides*, whereby behaviour, particularly during the warmer parts of the day during the wet season, or for approximately 8 months of the year during the dry season may result in tortoises going undetected as a result of partial burial or aestivation within the substrate (Walker et al., 2007; Walker, 2012). This can lead to underestimation of density (Buckland et al., 2001; Thomas et al., 2010).

Therefore, to allow a greater understanding of this species' population dynamics and establish a current baseline population estimate for the tortoise, this chapter details the results of a study to firstly assess detection probability of the species within its natural habitat during the wet season when the species is thought to be at its most active (Walker et al., 2007). Further to this, a line transect distance sampling procedure was applied across the species narrow coastal

range (Walker et al., in press) within southwest Madagascar. Subsequently the results are reported detailing the population density and size estimate firstly for the species as a whole, and secondly for the five sub species or intergrade populations of this species (see Chapter 2; Walker et al., in press).

Methods

Study area

Walker et al. (in press) and Walker (2010) recently established the current area of occupancy of the species through ground truthing 131 sites across the species' historic extent of occurrence described by Bour (1981) using a presence/absence survey technique. These data were then integrating into a GIS (see Chapter 2) detailing the current area of occupancy of the species. *P. arachnoides* currently inhabits eight areas of forest comprising a total area of occupancy of 2,463.8 km² (Walker, 2010; Walker et al., in press) (Table 2; Fig. 7; see Chapter 2). The species is divided into three subspecies (Chari et al., 2005; Pedrono, 2008) and two zones of intergradation have been identified between these subspecies (Walker, 2010; Rhodin et al., 2011; Walker et al., in press; see Chapter 2). *P. a. brygooi* occupies the north of the species range, comprising three fragmented populations north of the Manombo River; *P. a. arachnoides* occupies the range south of the Onilahy River to approximately 30km north of the Linta River (Fig. 7); and *P. a. oblonga* occupies the southernmost extent of the range around Cap Sainte Marie Special Reserve, stretching east through the coastal dunes to approximately 70km east of the Manambovo River (Walker, 2010; Rhodin et al., 2011; Walker et al., in press; Fig. 7). The two small intergrade populations are found within the transitional zones between *P. a. brygooi*

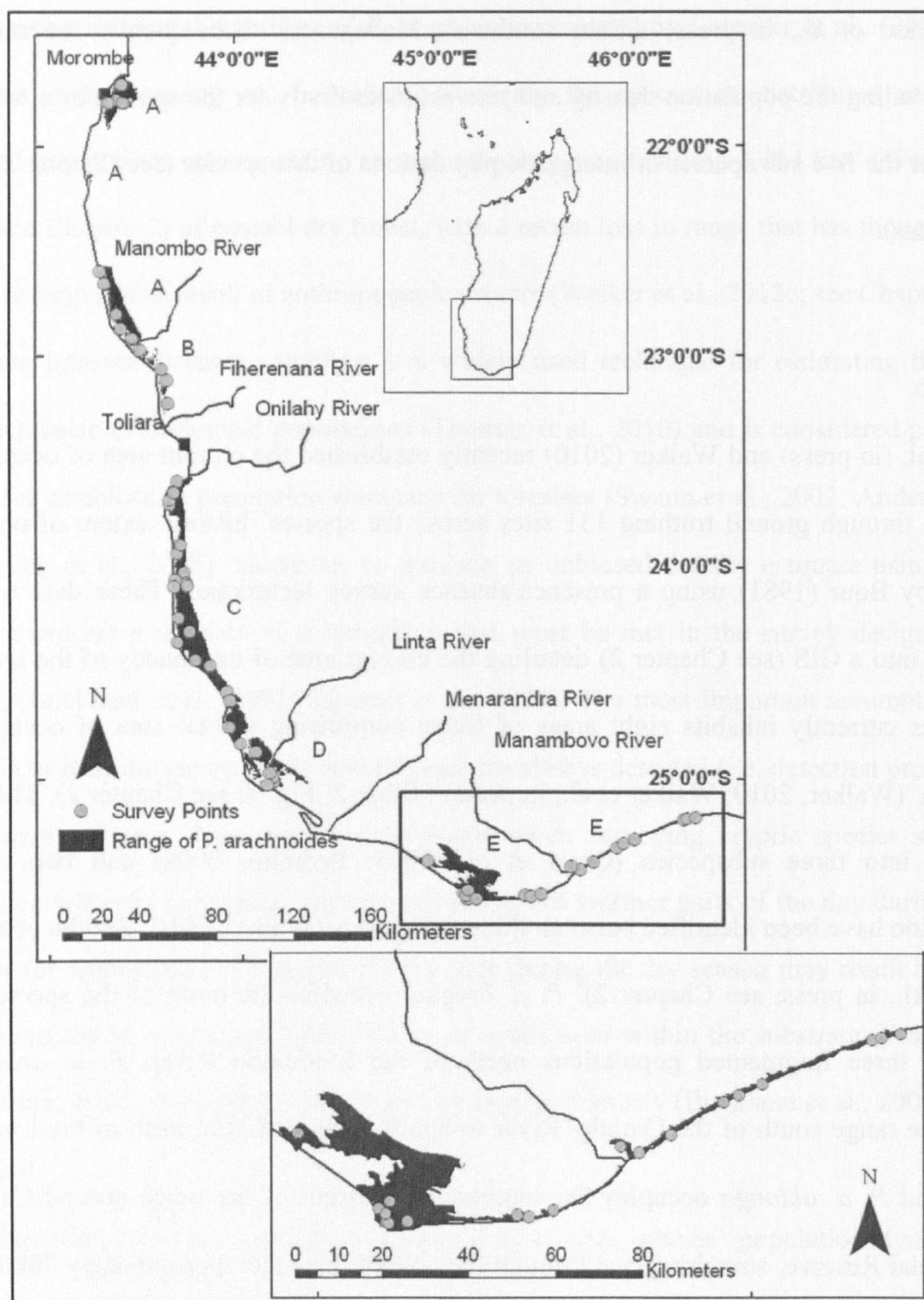


Figure 7: The 64 survey points displayed in addition to the current area of occupancy shown as eight areas of forest known to be occupied by *P. arachnoides* as described by Walker et al, in press and Walker (2010) (Chapter 2). A= three sub populations of *P. a. brygooi*, B= 1 sub population of *P. a. brygooi*/*P. a. arachnoides* intergrades, C= 1 sub population of *P. a. arachnoides* D= 1 sub population of *P. a. arachnoides*/*P. a. oblonga* intergrades, E= 2 sub populations of *P. a. oblonga*, showing a very narrow area, occupied to the east of the range (blow out).

and *P. a. arachnoides* (Walker, 2010; Rhodin et al., 2011) and between the ranges of *P. a. arachnoides* and *P. a. oblonga* (Walker et al., in press, Fig. 7).

Field techniques

Establishing detection probability

Walker et al. (2007) have established that field surveys undertaken during the austral winter, resulted in 55.1% lower detection levels for *P. arachnoides* than surveys undertaken during the warmer, damper summer months (November to April). However, the detection probability; $g(0)$ (i.e. the amount of time the tortoise remains visible during the summer months) is unknown and is critical in order to establish the effectiveness of any distance sampling survey (Buckland et al., 2001). To measure $g(0)$ nine tortoises were selected from the population within the forests of the Anakoa region (Walker et al., 2007) on separate days during February 2003 for continuous focal observations (Altmann, 1974; Martin & Bateson, 1993). Each tortoise was located at approximately 0600 h by searching at the base of low lying vegetation (Walker et al., 2012) on clear, cloudless days. Observers used 10× binoculars at an observation distance of c.10m to watch each tortoise for the whole day (06:30 h-18:30 h, Hailey & Coulson, 1999; Lagarde et al., 2003), undertaking three hour shifts. Observers recorded, in minute, intervals if the tortoise was visible or fully obscured from view.

Distance sampling

Line transects were used; a method widely applied in establishing population size and density estimates in an array of taxa (Newey et al., 2003; Rivera-Milan et al., 2004; Jathanna et al., 2008), including southern Madagascar's two other, dry forest tortoise species; *P. planicauda* and *Astrochelys radiata* (O'Brien et al., 2003; Leuteritz et al., 2005; Young et al., 2008). The

statistical routine used for analysing line transect data derived from distance sampling is based on Fourier analysis (Burnham et al., 1980; Akin, 1998), the accuracy of which depends on four assumptions: (1) objects directly on the line (at zero distance) will not be missed (i.e. $g(0)=1$); (2) objects are fixed at the initial sighting position (i.e., they do not move rapidly upon detection and are not counted more than once); (3) distances are measured exactly; and (4) all sightings are independent (Burnham et al., 1980). Tortoises lend themselves well to this method of estimation by not violating key assumptions of the model (Burnham et al., 1980; Akin, 1998; Leuteritz et al., 2005). However, *P. arachnoides* is known to aestivate seasonally; during the dry season from May to November (Walker et al., 2007) and also become dormant daily during the warmest part of the day between December and April, when the species is otherwise at its most active (Walker et al., 2007; Pedrono, 2008). Therefore, if surveys are undertaken at inappropriate times of the day and/or year assumptions 1 and/or 4 will be violated.

Table 2: Current known area of occupancy of the three subspecies and two intergrade populations of the spider tortoise (*Pyxis arachnoides*) in Madagascar (Fig. 1), with the subpopulations indicated by the letters A–E, which correspond to the locations labelled in Fig 1, the source of these data, and the number of transects used to survey each subspecies and intergrade population and the years in which the surveys took place.

Subspecies	No. of subpopulations	Area of occupancy (km ²)	Source	No. of transects	Year of survey
<i>P. a. brygooi</i> (A)	3	499.6	Walker (2010), Walker et al. (in press), Rhodin et al. (2011)	13	2009
<i>P. a. brygooi</i> / <i>P. a. arachnoides</i> intergrades (B)	1	99.7	Walker et al. (in press)	4	2009
<i>P. a. arachnoides</i> (C)	1	1,029.1	Walker et al. (in press)	22	2010
<i>P. a. arachnoides</i> / <i>P. a. oblonga</i> (D)	1	267.0	Walker et al. (in press)	6	2010
<i>P. a. oblonga</i> (E)	2	568.5	Walker et al. (in press)	19	2010/2011
Total	8	2,468.8		64	

Sixty four transects were selected across the species area of occupancy as described by Walker et al., (in press) and Walker (2010) (Table 2; Fig. 7). The locations of transects were generally evenly spread across this range within typically representative habitat (Fig. 7) and comprised of 63 1000m and one 600m transects. Field work was undertaken during January and February 2009, 2010 and 2011 during the annual period of highest tortoise activity (Walker, et al., 2007; Pedrono, 2008). Surveying was limited to between 0630 h–1030 h and 1530 h–1830 h during the cooler parts of the day to account for the species crepuscular behaviour (Walker et al., 2007).

Two observers traversed each transect walking side by side on an easterly bearing in a liner direction, using the tracking function of a handheld GPS to measure the distance. Each surveyor carefully searched for tortoises on their respective side of the transect line and directly in front them. The 1000m transects took on average 34.7 (± 5.1) minutes to traverse (not including the time spent stationary at the point when tortoises were detected) with time dependent upon terrain and density of the vegetation. Upon encountering an individual, the perpendicular distance from the centre of the transect line (where the observer was standing) was measured in cm to the middle of the carapace of the point of first detection for each tortoise, using a 15m steel retractable tape measure. Each tortoise was marked using a small dot of nail polish on the top of the carapace, to avoid duplicate counting.

Data Analysis

Establishing detection probability

The total number of minutes for which each of the nine tortoises were out of view were divided by the total number of minutes for the nine days within the following pre-determined periods;

0630 h-1030 h, 1030 h-1530 h and 1530 h-1830 h, and compared using a one-way ANOVA ($\alpha = 0.05$) with Tukey's post hoc test. Prior to analysis, data were tested for normal distribution using a Ryan-Joiner test and where necessary transformed using a Box-Cox transformation. All statistical analyses were performed using Minitab 12.

Distance sampling

Using Program Distance 5.0 software (Thomas et al., 2010) a Conventional Distance Sampling (CDS) engine was used to analyse the line transect data. The data comprised 109 objects (tortoises), of all size classes across the 64 transects. The probability of detection was modelled as a function of observed distance from the transect line using robust, semi-parametric methods. Initially, the perpendicular distance data for the 109 tortoises were examined in a histogram of 16 intervals of equal width to investigate any responsive movement (Laake, 1978) to the observer and clumping of observations (Fig. 8). No strong evidence of evasive movement was detected. However, distances further from the centre line (151-300cm) and data close to 0cm distance (<50cm) appeared to show some degree of over recording within these areas (Fig. 8). This was possibly a result of inconsistent detection in some areas due to the small size of tortoises (adult mean straight carapace length; 169 mm (± 23.3), Walker et al., 2007), cryptic behaviour of the tortoises and large variations in habitat complexity (Best, 1981). It was therefore necessary to truncate ($w = 700\text{cm}$) and transform data into automatically adjusted intervals, using the data filter function to gain a shoulder at 0cm distance (Fig. 9) and improve model robustness (Thomas et al., 2010). The following models, considered to be general and robust (Leuteritz et al., 2005; Young et al., 2008; Thomas et al., 2010), were run; uniform/cosine (Burnham et al., 1980), uniform/simple polynomial (Anderson & Pospahala, 1970), half-normal/hermite polynomial and hazard-rate/simple polynomial (Buckland, 1985) models. Model fit was assessed using Akaike's

Information Criterion (AIC) values, trading off the bias of simple models against the higher variance of more complex models (Thomas et al., 2010). Finally, the fit of the model was tested using Chi squared (χ^2) goodness of fit test.

Densities and population estimates were produced for each of the three subspecies and each of the two intergrade populations (Table 2). To improve model precision the probability of detection (p) and the SE of p , calculated from the global detection function (Buckland et al., 2001) of the whole population model was added as a multiplier field to these data. The analysis was re-run, post stratifying the data by the five subspecies or intergrade populations, using the same four models as were used for the whole population model. Data were truncate ($w = 700\text{cm}$) and transform into automatically adjusted intervals, using the data filter function (Thomas et al., 2010). The four models were interrogated as a whole and the best fitting density and population estimates for each individual subspecies/intergrade population were picked from across the four models.

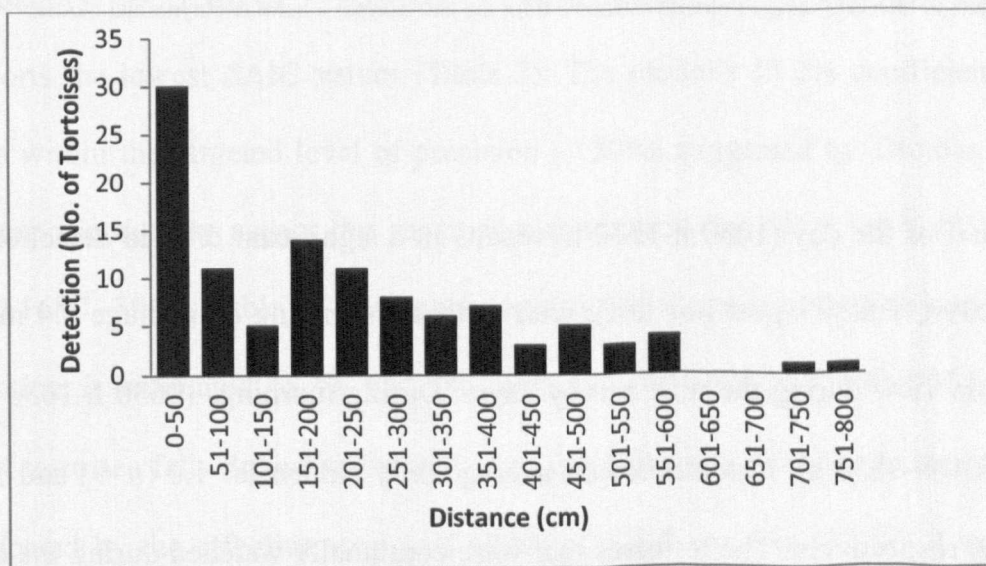


Figure 8: Raw distance data for the entire population of *P. arachnoides* grouped into 50cm intervals showing over recording at 151-300cm, and a spike at 0cm distance as a result of varying detection probability further from the centre line due to variation in habitat complexity and the small size of the species.

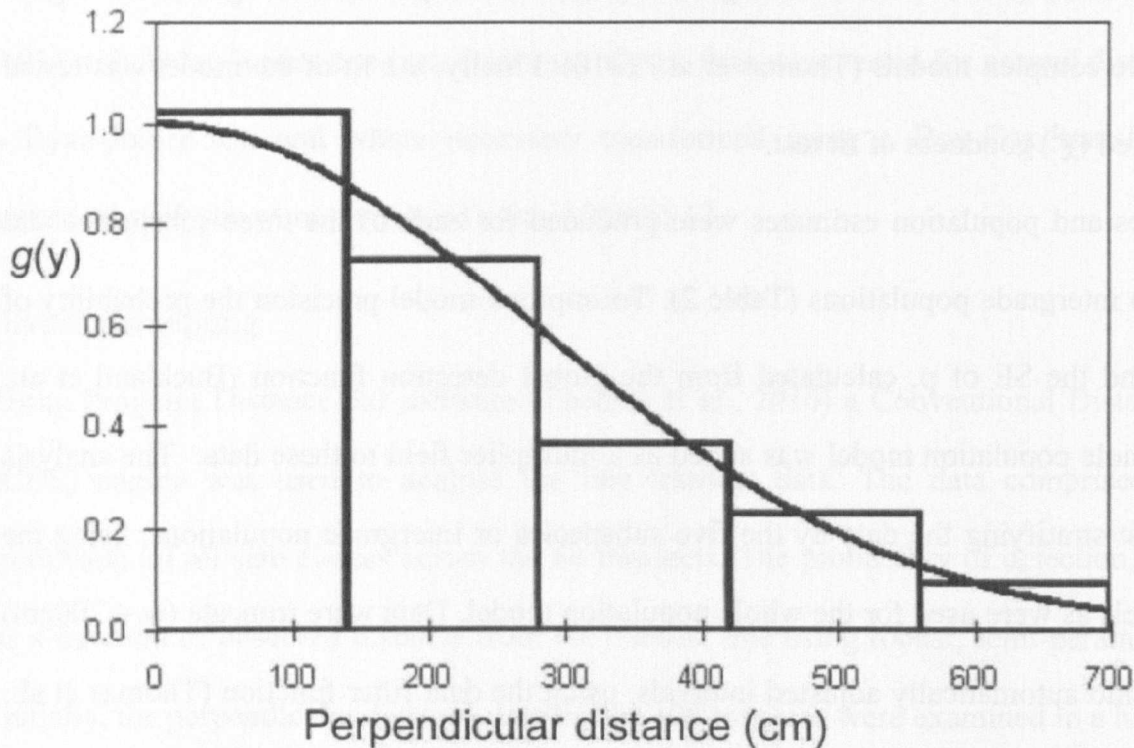


Figure 9: Data detection probability $g(y)$ for data comprising the entire population of *P. arachnoides* after truncation and transformation of data to intervals using Program Distance 5.0 for the half-normal + hermite polynomial model.

Results

The warmer part of the day (1030 h-1530 h) results in a significant drop in detection (one-way ANOVA $P=0.019$, Tukey's post hoc test), with tortoises spending on average 5.4 minutes ($n = 49$) hidden from view during the nine survey days. During mornings (0630 h-1030 h) and late afternoons (1530 h-1830 h), tortoises are on average only hidden for 1.0 ($n=9$) and 1.6 minutes ($n=13$, Fig. 10) respectively. The tortoises that were continually watched during the cooler parts of the day had a detection probability of 1, therefore negating the need for a multiplier to be added to the distance data.

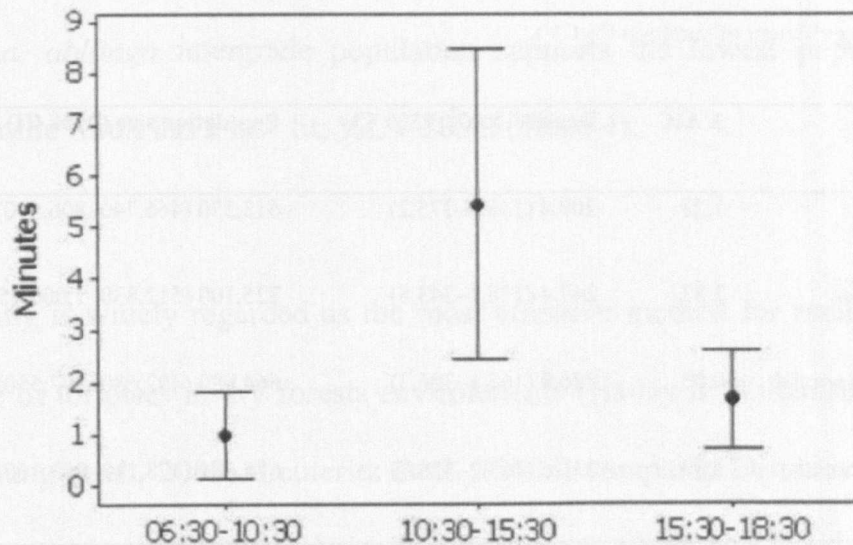


Figure 10: Mean number of minutes during three time intervals (0630h-1030h, 1030h-1530h and 1530h-1830h) when nine individual tortoises were hidden to the observer.

The half-normal + hermite polynomial adjustment model proved a good fit to the species population data ($\chi^2 = 1.10$, $df = 3.00$, $P = 0.78$) within the CDS model. This adjustment model supports the lowest ΔAIC values (Table 3). The model's 15.2% coefficient of variation (%CV) falls within the targeted level of precision (< 20%) suggested by Thomas et al. (2010). The mean tortoise density across the range is estimated to be 226.9 km^{-2} (95% confidence interval (CI) 168.1–306.3; Table 3). Using this density and the area of the known total range, the total population is estimated to be 664,980 tortoises (95% CI, 492,680–897,550; Table 3). Detection of tortoises falls dramatically with increasing distance from the centre of the transect line, as indicated by the effective strip half width of 340.7 cm (Fig. 9), i.e. it was difficult to detect tortoises >3 m away from the centre line of the transect.

When the data were post stratified by sub species and intergrade populations and run again the results become less robust due to the high %CV (Table 4). The Uniform + constine or

Table 3: Each of the four Distance models used to estimate the whole population of spider tortoises, with corresponding ΔAIC , mean density per km^{-2} (with upper and lower 95% confidence limits), mean population size (with upper and lower 95% confidence limits) and % coefficient of variation (% CV).

Model	ΔAIC	Density km^{-2} (95% CI)	Population size (95% CI)	% CV
Uniform + cosine	1.23	209.4 (159.3–275.2)	613,570 (466,740–806,590)	13.82
Uniform + simple polynomial	2.87	247.4 (178.1–343.8)	725,100 (512,830–1,000,750)	10.44
Half- normal + hermite polynomial	0.00	226.9 (168.1–306.3)	664,980 (492,680–897,550)	15.23
Hazard rate + simple polynomial	1.39	231.6 (163.2–328.7)	678,600 (478,110–963,160)	12.15

Table 4: Each of the four Distance models used to estimate the population of spider tortoises post stratified by sub species/intergrade populations displaying the model which provides the most robust fit for each population with corresponding, mean density per km^{-2} (with upper and lower 95% confidence limits), mean population size (with upper and lower 95% confidence limits) and % coefficient of variation (% CV).

Subspecies/integrate population	Most suitable model	Density km^{-2} (95% CI)	Population size (95% CI)	% CV
<i>P. a. brygooi</i>	Uniform + cosine	76.5 (11.2–524.3)	224,940 (32,824–1,541,600)	126.7
<i>P. a. brygooi/P. a. arachnoides</i>	Hazard rate + simple polynomial	20.5 (3.9–106.8)	60,301 (11,579–314,040)	101.5
<i>P. a. arachnoides</i>	Uniform + simple polynomial	32.7 (6.7–159.8)	96,242 (19,714–469,850)	96.1
<i>P. arachnoides/P. a. oblonga</i>	Uniform + cosine	4.5 (0.80–25.4)	13,264 (2,354–74,730)	108.3
<i>P. a. oblonga</i>	Uniform + cosine	10.7 (2.2–54.0)	31,350 (6,195–158,640)	53.6

simple polynomial adjustments generally provide the best fit for four of the five groups (Table 4). The most robust result appears to be for *P. a. oblonga* with a goodness of fit equalling; $\chi^2 =$

3.21, $df = 3.00$, $P = 0.361$. *P. a. oblonga* supports the smallest population of the three subspecies of 31,350 (CI 6,195-158,640) at a density of 10.7 (CI 2.2-54.0) per km^2 . Whilst the *P. a. arachnoides*/*P. a. oblonga* intergrade population supports the lowest population of all five groups, however the result has a low fit; %CV 108.3 (Table 4).

Discussion

Distance sampling is widely regarded as the most effective method for establishing population density estimate of tortoises in dry forests environments (Hailey & Willemsen, 2000; Anderson et al., 2001; Young et al., 2008). Leuteritz et al., (2005) compared Distance sampling with the Lincoln–Petersen mark re-capture technique (Greenwood, 1996) and concluded that the latter method was prone to over estimation when applied to the *A. radiata* in southwest Madagascar. The half normal model used in this study is known to perform well with data that show a rapid fall in detection (Newey et al., 2003; Thomas et al., 2010) as Figure 9 shows. This model works well for data collected on cryptic animals surveyed in areas of thick and patchy vegetation cover (e.g. Rivera-Milan et al., 2004), such as *P. arachnoides*.

These data represent the first baseline assessment of the population size and density for the species across the whole range, with this studies' figure of 664,980 (95% CI 492,680–897,550) falling somewhere between the two previous estimates of 2-3 million (Pedrono, 2008) and 282,000 (Randriamahazo et al., 2007). Generally, population size and density estimates for other small, arid environment tortoises appear to be lacking, so inter-species comparisons are difficult. However, Young et al., (2008) reported a global population estimate of approximately 28,000 *Pyxis planicauda*, very sparsely distributed (0.4 individual per ha.) across the species' narrow range.

The estimates for the populations post stratified by subspecies or intergrade population have resulted in a less robust result than data analysed as a pooled population, with high confidence intervals and high %CV (Table 4). These results have come about as an effect of either low sample size or irregular densities of tortoises within certain areas and precision could be improved through increased sampling effort. However, the limited time that the tortoises are active and visible either during the day or the year (Walker et al., 2007) and the logistical challenges of working within this environment often limits the amount of possible sampling effort. Small numbers of observations, as is the case when the data is post stratified by population can also result in less information with which to judge whether the modeled detection function is a reasonable approximation of how detection probability of tortoises declines with distance (Young et al., 2008; Thomas et al., 2010). Indeed this study has not taken into account that there could be possible variations within the detection of tortoises between subspecies or geographical region which could affect $g(0)$ as our estimation of $g(0)$ was based from just nine individual *P. a. arachnoides*. Despite this, populations potentially as low as 2,300 and 11,500 respectively, for the two intergrade populations is cause for concern, if current genetic and morphological diversity is to be preserved within the species (Rioux Paquette et al., 2007).

All previous population density studies for spider tortoises have lacked spatial resolution and have been confined to geographically small areas. Walker et al., (2007) and Jesu & Schimmenti (1995) report densities for *P. a. arachnoides* of 4.6 (± 1.6) individuals per ha. and approximately 3.0 individuals per ha. respectively in the Anakao region, with field work undertaken during the same time of year as the research presented here, using sweep searches or simple belt transects. Pedrono (2008) notes during field trips to *P. a. oblonga*'s range, finding densities of upwards of 16 individuals/ha, using sweep searches in areas of good habitat. In

comparison the data presented in this study reveals a mean range wide density estimate of 2.3 (95% CI 1.7-3.1) individual per ha. (Table 3).

The dry coastal forests of southwest Madagascar are one of the country's most threatened terrestrial habitats, with habitat loss recorded at 1.2% per year (Harper et al., 2007) between 1990 and 2000 across the habitat as a whole and currently at 1.2% per year within the core of *P. arachnoides*' range (see Chapter 5; Walker et al., in press). Habitat loss has resulted in severe fragmentation of the current area of occupancy of the species (see Chapter 2; Walker et al., in press; Walker, 2010), which has probably resulted in a reduction of population size and density within the last few decades. Habitat fragmentation could potentially have wide ranging conservation impacts for the remaining populations of *P. arachnoides* with direct effects often resulting in altered age structures within populations of chelonians (Aponte, et al., 2003). Indeed, the problem of habitat fragmentation may increase as a result of the proposed widespread resource extraction activities planned within the southwest (see Chapter 2; Walker et al., in press). In an effort to bring much needed economic prosperity to the region the government has released mining concessions to allow the proposed exploitation of mineral sands throughout much of coastal southwest Madagascar (Sarrasin, 2006).

The results of this study can be considered important in the management of this threatened species, as establishing population size of a threatened species is often considered one of the most important factors in the management of such species (Buckland et al., 2001), whereby results can be used as a baseline for future population monitoring through the revisiting of original survey sites (Young et al., 2008). Currently, habitat loss resulting from subsistence agriculture and fuel wood harvesting is the greatest driver responsible for the decline in spider tortoises (see Chapter 5; Pedrono, 2008; Walker et al, in press). Therefore, the most challenging

issue to address will be the socioeconomic and cultural issues causing local communities to harvest timber from the coastal dry forests habitat of this species.

Chapter 4: Survival probability of a population of Madagascar spider tortoises (*Pyxis arachnoides*)⁷

Introduction

The Critically Endangered spider tortoise *Pyxis arachnoides* (Leuteritz & Walker, 2009), endemic to Madagascar's southern coastal, dry forests, is thought to be facing significant threats to its long term survival, predominantly as a result of habitat loss (Seddon et al., 2000; Walker et al., 2007; Pedrono, 2008). This has resulted in recent years, in range contraction (see Chapter 2; Walker, 2010; Walker et al., in press; Fig. 11). However, very little is known about this species' biology, ecology or life history (Walker et al., 2007; Pedrono, 2008) within its coastal southern dry forest habitat, which supports some of the highest rates of endemism in Madagascar (Fenn, 2003; Seddon et al., 2000). Habitat loss within this region was estimated to be 1.2% per year during the period 1990-2000, mainly as a result of unsustainable, subsistence agricultural practices (Harper et al., 2007), with little sign of the habitat loss abating (Walker et al., 2012c).

Age or stage specific survival is a key demographic component of the population growth and evolutionary fitness of any species (Fox 1993; Coulson et al., 1997), with this knowledge considered particularly important for the management of threatened chelonian species (Bowen et al., 2004). Indeed, assessing the demographic health of a tortoise population often begins with assessing adult mean survival of a population, on account of the growth rate of a population being dependent upon adult survival, regardless of reproductive rates, due to the longevity of most species (see Chapter 5; Heppell, 1998; Walker et al., 2012c).

⁷ Walker, R.C.J., Luiselli, L & Rafeliasoa, T.H. (2012) Survival probability of a population of Madagascar spider tortoises (*Pyxis arachnoides*). *Amphibia Reptilia* 33, 141-144. – Appendix 1

Cormack-Jolly-Seber (CJS) capture-mark-recapture (CMR) models are useful for assessing the survival parameters of a population based on the prevailing biotic and abiotic factors that the population is subjected to (Hestbeck, 1995). Very few studies have assessed the survival probability of a population of chelonians within a habitat intensively exploited by humans (Bowen et al., 2005). These resulting age or stage based survival data can then be used for modelling projected survival for a particular population into the future (i.e. see Chapter 5; Caswell, 2001) and can be vitally important in directing targeted conservation efforts to focus sympathetic management techniques to a particular target cohort within a given population of tortoises. Despite the importance of determining annual survival of wild chelonian populations, reliable survival data is often lacking for many species (Bjorndal et al., 2003). In this chapter a stage and sex based, mean annual survival analysis using a CJS method derived from a three year CMR sampling program for a population of *P. arachnoides*, within the core of the species narrow coastal range is presented. The results of this work will allow an assessment to be made as to the conservation risk facing the population.

Methods

Study area

A c. 10.2km² patch of southern dry forest habitat, (southwest corner: -23°40' 40.7748'S, 43°39'52.0266'E; northeast corner: -23° 40'42.6102'S, 43°43' 29.9922'E), c. 3km east of the coastal fishing community of Anakao and south of the provincial capital Toliara, within the core of the species range was selected as the study site (Fig. 11). The site comprises patchy xerophytic scrub, typical of the region south of the Onilahy River (Fenn, 2003) (Fig. 1) and is known to support a representative population of tortoises at a density of 4.6 (SE ±1.6) tortoises per ha. with

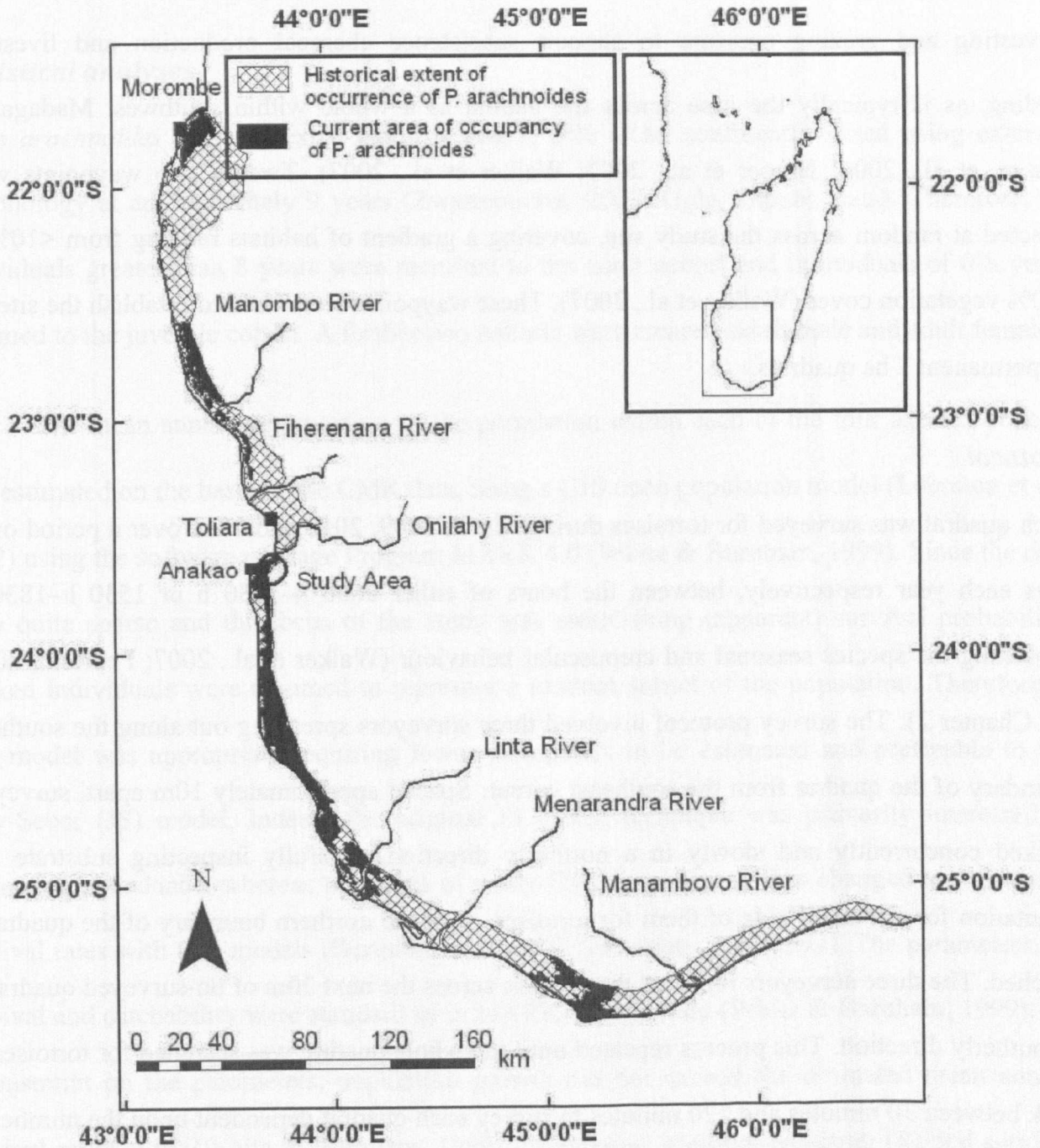


Figure 11: Study site c. 3km east of the coastal community of Anakao within the core of the species range, within the coastal dry forests of southwest Madagascar. *P. arachnoides*' area of occupancy is represented in black (Walker et al., in press), with the former extent of occurrence described by Bour (1981) and Pedrono (2008) represented by cross hatch.

all age cohorts represented within the population (Walker et al., 2007; Walker & Rafeliasoa, 2012). The vegetation within the study area has been subjected to moderate but sustained harvesting and grazing pressure to support subsistence charcoal production and livestock herding, as is typically the case across the habitat as a whole within southwest Madagascar (Casse, et al., 2004; Harper et al., 2007; Walker et al., 2007). Twenty two waypoints were selected at random across the study site, covering a gradient of habitats ranging from <10% to >90% vegetation cover (Walker et al., 2007). These waypoints were used to establish the sites of 22 permanent 1 ha quadrats.

Protocol

Each quadrat was surveyed for tortoises during March 2009, 2010 and 2011 over a period of 10 days each year respectively, between the hours of either 0600 h–1030 h or 1530 h–1830 h, exploiting the species seasonal and crepuscular behaviour (Walker et al., 2007; Pedrono, 2008; see Chapter 2). The survey protocol involved three surveyors spreading out along the southerly boundary of the quadrat from the southeast corner. Spaced approximately 10m apart, surveyors walked concurrently and slowly in a northerly direction, carefully inspecting substrate and vegetation for 5m either side of them for tortoises, until the northern boundary of the quadrat is reached. The three surveyors repeated the process across the next 30m of un-surveyed quadrat in a southerly direction. This process repeated until the whole quadrat was searched for tortoises. It took between 30 minutes and 120 minutes to survey each quadrat dependent upon the number of tortoises encountered.

Upon detection, each tortoise was sexed, if age allowed, using the external morphology of the lower plastron and tail length as described by Walker et al., (2007) and aged using the

scute annuli counting technique described by Germano (1998). Finally, each tortoise was marked using a unique carapace notching code (Cagle, 1939).

Statistical analyses

Pyxis arachnoides reaches sexual maturity and is able to be confidently sexed using external morphology at approximately 9 years (Zwartepoorte, 2003; Ogle, unpubl. data). Therefore, all individuals greater than 8 years were recruited to the adult cohort and individuals of 0-8 years assigned to the juvenile cohort. A further two cohorts were created; adult male and adult female.

The mean annual survivorship of the population within each of the four age/sex cohorts was estimated on the basis of the CMR data, using a CJS open population model (Lebreton et al., 1992) using the software package Program MARK 4.0 (White & Burnham, 1999). Since the data were quite sparse and the focus of the study was establishing (apparent) survival probability, marked individuals were assumed to represent a random subset of the population. Therefore, a CJS model was appropriate requiring fewer parameters to be estimated and preferable to the Jolly-Seber (JS) model. Indeed, the original JS model technique was primarily interested in estimating abundance, whereas the focus of many CMR experiments has changed to estimating survival rates with CJS models (Bertolero et al, 2007; Lebreton et al., 1992). The parameters for survival and catchability were standard as in MARK 4.0 software (White & Burnham, 1999). As a constraint on the parameters, population growth did not exceed the estimated mean annual survival probability (White & Burnham, 1999). In addition, constant recapture (R) and survival (S) probabilities were assumed, to avoid confounding of the parameters, given the short duration of the study (Lebreton et al., 1992; White & Burnham, 1999). The 95% confidence intervals (CI) for mean annual survival and for mean probability of capture were calculated by the formula: $\bar{x} \pm t^* \times SE$ where \bar{x} is the point estimate, t^* is the critical value from the t-distribution (1.96

in our case, given the relatively large sample sizes, and probability 0.025), and SE = the standard error. The upper 95% CI was truncated to =1.0.

Results

A total of 404 captures over three years have been made for 360 tortoises (adults $n=246$; adult males $n=110$, adult females $n=136$; and juveniles $n=114$). Despite the large sample size, the CMR profile frequencies are relatively sparse with 87.8% ($n=316$) of the tortoises captured once, 11.7% ($n=42$) captured twice and 0.6% ($n=2$) captured three times. As a result, recapture rates for the juvenile and adults split by sex cohorts are too low for survival estimates to be established. Mean annual survival for the adult cohort is estimated to be 0.823 (SE \pm = 0.15; 95% CI = 0.565-1.0) with a mean probability of capture of 0.132 (SE \pm = 0.034; 95% CI = 0.065-0.199).

Discussion

Other comparative studies documenting the survivorship of other small, dry forest tortoise species are generally scant (Willemsen & Hailey, 2001; Loehr, 2010) and studies showing the effects of anthropogenic habitat alteration are even more limited. Loehr (2010) documents annual mean survivorship figures of 0.74 (± 0.07) to 0.99 (± 0.03) for a *Homopus signatus* population under natural conditions. A population of *Testudo hermanni* from Greece supported an overall annual mean population survivorship of just 0.5 (± 0.05), when the population was subjected to mechanical habitat destruction (ploughing and bulldozing), with the greatest effects to juvenile tortoises (Hailey, 2000). However, adult annual mean survivorship of spider tortoises within this study fared similarly to adult *T. hermanni* (0.88, ± 0.04) in the Greek study, at a site that was considered to support natural conditions (Hailey, 2000). Comparatively, populations of the same species in Spain supported higher survivorship (0.95 ± 0.01) than this

studies' population of spider tortoises (Bertolero et al., 2007). However these results must be interpreted with caution when undertaking comparisons with other studies for similar species, on account of the minimal study period of just three years and the quite large SE of mean annual survivorship compared to other studies. Dodd & Dreslik (2008) have shown within their work that habitat disturbance can have negative effects through altering growth rates and the onset of sexual maturity amongst box turtles *Terrapene carolina bauri*. Whist in Madagascar O'Brien et al. (2005) report that larger hatchling *Astrochelys yniphora* have a significantly greater chance of surviving the first year of life than the smaller portion of the cohort and mature animals support a mean annual survival rate of 0.97 (SE ± 0.06) (O'Brien et al., 2005).

Adequate recapture rates was a limiting factor of this study, particularly in obtaining data to allow for mean annual survival estimates for the juvenile cohort within the population. This could be avoided in future work through condensing the survey plots to a smaller geographical area or increasing the number of plots within un-sampled gaps, within the forest. This would allow animals which wander off the survey plot where they were originally marked a greater chance of recapture. A longer sampling period over more years, as suggested by Lebreton et al. (1992), could also improve model robustness. Pike et al. (2008) suggest some limitations particularly for establishing the demographics of animals within the juvenile phase. In studies where sufficient numbers of juveniles are encountered to allow modelling, survival rates among juvenile reptiles are often significantly underestimated, due to poor detection rates and subsequent re-capture as a result of cryptic behaviour (Pike et al., 2008). More open habitats such as dune type habitats appear to allow for greater juvenile tortoise recapture rates (Fernández-Chacon et al., 2011).

Pedrono (2008) and Walker & Rafeliasoa (2012) suggest that the spider tortoise is absent or occurs in sparse numbers in disturbed habitat, a hypothesis supported by anecdotal observations with this study area. It is possible that this population of tortoises is subjected to habitat loss-related stress and subsequently the adult survivorship presented here may represent an unnatural state. The exact level to which habitat loss affects spider tortoise survivorship is difficult to establish. No control population exists within this study area, with control sites generally difficult to establish because of widespread anthropogenic loss of this habitat. Indeed, southern dry forest is threatened even within officially protected areas (Harper et al., 2007) and areas protected under local taboo or community convention (Bodin et al., 2006). However, future research efforts should focus sampling effort across quadrats supporting a gradient of habitat degradation. Further studies detailing the long-term effects of habitat loss and degradation on the demography of the spider tortoise will be an important component of conserving this Critically Endangered species.

Chapter 5: The effect of habitat deterioration on the long term survival of the Critically Endangered Madagascar spider tortoise (*Pyxis arachnoides*)⁸

Introduction

Chelonians are considered to be one of the most threatened taxon, with 67% of the remaining species thought to be threatened with extinction, as a result of habitat loss, harvesting or other human induced disturbances (Rhodin et al., 2011). Many of these species inhabit tropical forest landscapes, which from a global perspective are becoming increasingly fragmented as a result of anthropogenic pressures (Achard et al., 2002). From a theoretical perspective, habitat loss is often predicted to result in abrupt changes in the distribution and survival of populations of organisms and a reduction in biodiversity (Lande 1987; Tilman et al., 2002). However, there remains a lack of applied research into the effects of habitat loss on the population dynamics of tortoise species in general (Aponte et al., 2003).

The dry coastal forests of southern coastal Madagascar support some of the highest rates of endemism within the country (Fenn, 2003; Harper et al., 2007) and are therefore globally important to biodiversity conservation (Seddon et al., 2000). However, this habitat has experienced levels of forest loss of 1.2% per year between 1990 and 2000 (Harper et al., 2007), due mainly to small scale agriculture and charcoal production (Fenn, 2003; Bodin et al., 2006; Harper et al., 2007) and low levels of formal protection compared to other habitats within Madagascar (Seddon et al., 2000; Gardner, 2009). These anthropogenic pressures coupled with

⁸ Walker, R.C.J., Whitmore, N., Rafeliasoa, T.H. & Hamylton, S. (2012) The effect of habitat deterioration on the long term survival of the Critically Endangered Madagascar spider tortoise. *Biological Conservation*, 152, 152-158. - Appendix 1

limited management make it important to establish the effects of forest removal upon regionally endemic, rare species.

Eight relict populations of the Critically Endangered Madagascar spider tortoise (*Pyxis arachnoides*) are confined to this dry coastal forest ecoregion covering a total area of occupancy of 2,463.8 km² (Walker, 2010; Walker et al in press; Walker & Rafeliasoa, 2012; see Chapter 2) (Fig. 12a). The species is divided into three subspecies (Pedrono, 2008) with two zones of intergradation between these subspecies (Walker, 2010; Walker et al., in press; see Chapter 2). *P. arachnoides* remains Madagascar's least studied endemic chelonian species (Walker, et al., 2007; Pedrono, 2008; Walker, 2010). However, the restricted range suggests the species has specific habitat requirements (Walker et al., 2007; Pedrono, 2008), favouring areas with <45% canopy cover (Walker et al., 2007), with juvenile animals having a preference for higher vegetation cover (Walker et al., 2012a).

A number of powerful population modelling tools have been developed to assess the real time population status of a particular species (White & Burnham, 1999; Thomas et al., 2010). These models have often been used as effective conservation tools, guiding the strategies of conservation practitioners (Bjorndal et al., 2003; Young et al., 2008). Furthermore, the development of population matrix modelling, an analytical technique that allows the response of a population of a particular species to be modelled and projected into the future based on survival, life history and fecundity has become popular with conservation biologists (Caswell, 2001). Matrix modelling is a particularly useful conservation management tool when applied to species subjected to some form of anthropogenic stress, with the subsequent response to this stress quantified, in the form of altered survival or fecundity (Lamberson et al., 1992).

Assessing the extinction risk to any Critically Endangered species is essential if informed decisions are to be made regarding policy or conservation initiatives affecting the species in question. Currently there is a lack of such available data driving forward such initiatives for any of Madagascar's threatened tortoises species (Mittermeier et al., 2008) despite many conservationists predicting an imminent chelonian global extinction crisis (Rhodin et al., 2011). Using high resolution remotely sensed imagery, recent local vegetation loss for a region supporting a population of spider tortoises is quantified (Walker et al., 2007; Walker & Rafeliasoa, 2012). Further to this, this study presents the results of an eight year population monitoring exercise (2003, 2009, 2010 and 2011), applying data detailing the life history traits of this study population to a population matrix model, in an effort to quantify the extinction risk to this population of tortoises as a result of habitat degradation.

Methods

Study area

A c. 37.7km² patch of southern dry forest habitat, with the centre in the following location; 23°40' 40.7748 E, 43°39'52.0266 N, c. 3km east of the coastal fishing community of Anakao and south of the provincial capital Toliara, was selected as the study site (Fig. 12a). The site comprises of patchy xerophytic scrub (Fenn, 2003), with the area known to support a populations of *P. arachnoides*, of a density of 4.6 (± 1.6) individuals per ha. (Walker et al. 2007; Walker & Rafeliasoa, 2012). The vegetation within the study area has been subjected to moderate but sustained harvesting and grazing pressure to support small scale charcoal production and livestock herding (Casse, et al., 2004; Harper et al., 2007).

Anakao's prospering, fledgling tourism industry (Chaboud et al., 2004), coupled with a local taboo preventing the collection of tortoises (pers. obs.) has thought to have reduced tortoise

harvesting as a source of income within this region compared with sites north of Toliara within the Mikea forest region (Pedrono, 2008; Walker, 2010), or further south of Anakao (Woods-Ballard & Fanning, 2004) (Fig. 12a).

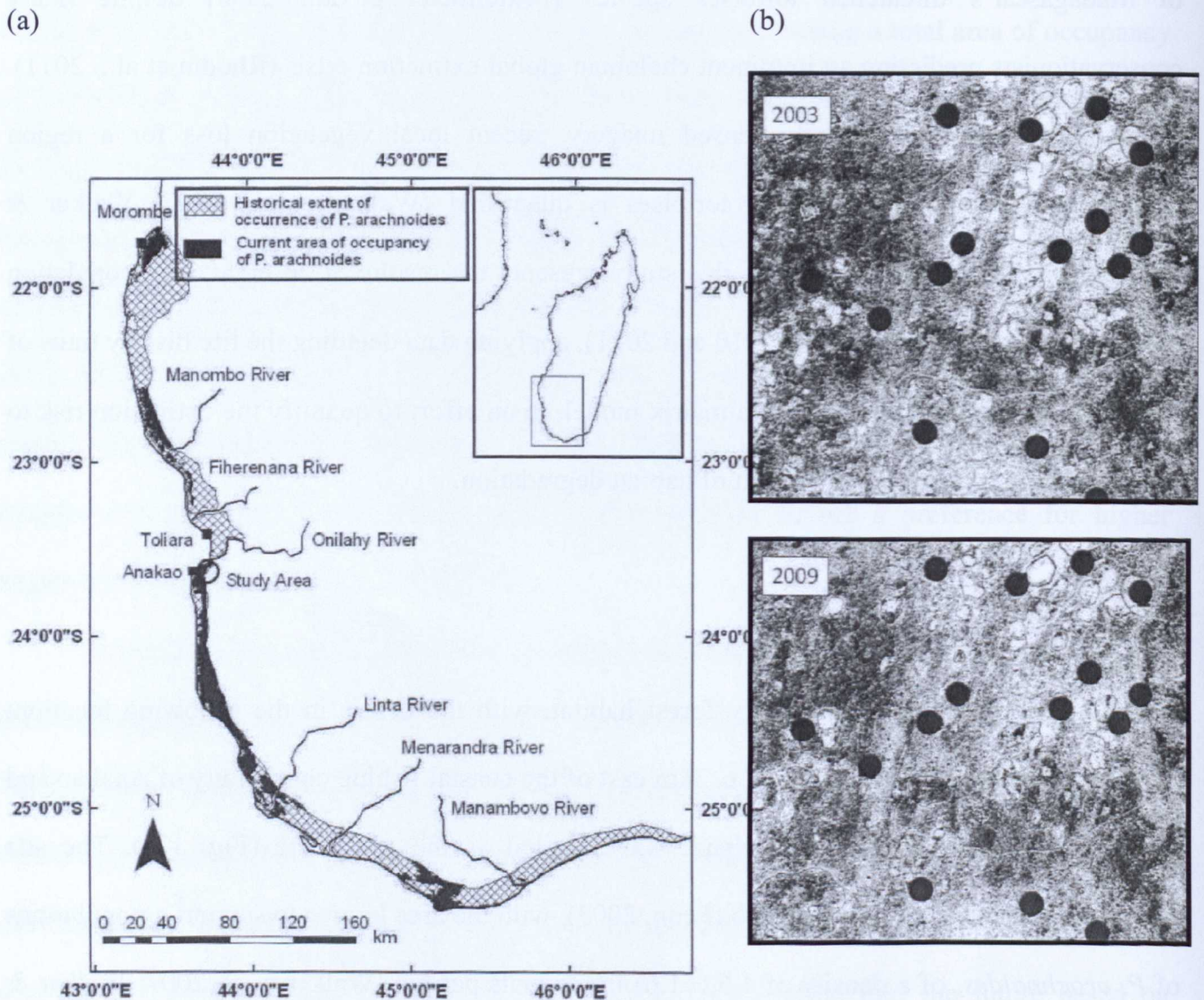


Figure 12: (a) Study site within the core of *P. arachnoides* coastal dry forest range, southwest Madagascar. Range map showing current area of occupancy adapted from Walker & Rafelarisoa, (2012) against the former historical extent of occurrence (Bour, 1981). (b) fifteen survey quadrats demarked by black dots overlaid on IKONOS 2 forest cover data for 2003 and 2009, livestock corrals and patches of land cleared for cultivation can clearly be seen as pale patches compared to the darker areas of natural vegetation.

Field techniques

Fifteen waypoints were selected at random within the study site. These way points were used to establish 15 permanent 1 ha quadrats (Fig. 12b). Each quadrat was surveyed for tortoises during March 2003, 2009, 2010 and 2011 over a period of eight days each year respectively, between 0600 h–1030 h or between 1530 h–1830 h, exploiting the species seasonal and crepuscular behaviour (Walker, 2012).

The surveying protocol involved three surveyors spreading out along the southern boundary of the quadrat at the south easterly corner. Spaced approximately 10m apart, each surveyor then walked concurrently, in a northern direction, carefully inspecting substrate and vegetation for up to 5m either side of them for tortoises, until the northern boundary of the quadrat was reached. The three surveyors would then repeat the process across the next 30m of unsurveyed quadrat, in a southern direction. This process was repeated until the whole quadrat had been searched for tortoises. Upon detection, each tortoise was aged using the scute annuli counting technique as described by Germano (1998).

Analysis techniques

Analysis of remotely sensed forest cover data

Two sets of IKONOS 2 satellite images were acquired for the study area, encompassing c. 37.7km² of remotely sensed ground cover data from images produced during March 2003 and March 2009 respectively (Fig. 12b). These data were subjected to a ‘dark pixel subtraction’ atmospheric correction to remove unwanted artefacts such as light scattered into the sensor from the atmosphere (Mather, 1999). The reflectance statistics of the darkest pixels in the image were extracted as an approximation of the contribution of light that was scattered into the sensor field of view by the atmosphere. Fifty pixels were exported from dark areas on satellite images from

both years and the mean reflectance of each waveband for the exported data was subtracted from the overall image data.

An unsupervised classification was applied to each image (Schowengerdt, 1997), whereby ground surface pixels of statistically similar reflectance character, were classified into 20 classes for each image. Given the similar spectral reflectance properties of surface coverage within the sensor field of view, these were subsequently reduced into 'vegetation' and 'non-vegetation' cover for each image. All image analysis and manipulation were undertaken using Erdas Imagine 8.5.

To validate image classification, co-ordinates were produced within the study site, identifying additional sites to be visited to facilitate interpretation and accuracy assessment of the classification output. Field survey teams made a record of the general characteristics of the area around each co-ordinate. Overall accuracy (%) was assessed for the classified map by calculating the proportion of points visited in the field that were correctly classified on the forest cover maps.

Following this, the total vegetation cover class for each quadrat was compared by year using a paired *t*-test ($\alpha = 0.05$). In addition to this, forest cover across the whole c. 37.7km² site for each year were compared. Prior to analysis, all data were tested for normal distribution (Ryan-Joiner) and adjusted using a Box-Cox transformation. Minitab 14 was used for data transformation and analysis.

Analysis of field data

Each of the tortoises recorded across the 15 quadrats for each of the four years was assigned one of three age classes, based on the number of scute annuli recorded; adult >8, sub-adult 8-4 and juvenile <4. The mean number of tortoises recorded for each for the three age classes, plus a

class which included all individuals recorded for each quadrat, for each of the four years was established. Following this the mean of each of these four classes were analysed using a linear regression analysis ($\alpha = 0.05$) to establish if population density within any of the classes had changed over time. Prior to regression analysis, all data were tested for normal distribution (Ryan-Joiner) and adjusted using a Box-Cox transformation. Minitab 14 was used for data transformation and analysis.

Table 4: Real and surrogate data for the construction of the *P. arachnoides* matrix. †= calculated mean survival from 16 surrogate species of chelonian taken from Pike et al. (2008).

Age	State	Survival value	Uncertainties	Species / Surrogate	Reference
Month 1-9	Egg	0.726	-	<i>Astrochelys radiata</i>	Jutta Hammer (pers comms)
Month 10-12	Hatchling	0.650	SE±0.2	†	Pike et al. (2008)
Year 2-3	Juvenile	0.650	SE±0.2	†	Pike et al. (2008)
Year 4-8	Subadult	0.750	SE±0.2	<i>Homopus signatus signatus</i>	Loehr (2010)
Year >8	Adult	0.823	SE±0.15; 95% CI 0.565-1.0	<i>Pyxis arachnoides</i>	Walker et al. (2012b), see Chapter 5
-	Adult fecundity	2.500	-	<i>Pyxis arachnoides</i>	Zwartepoorte (2003), Pedrono & Smith (in press), Michael Ogle (pers comms)

Population matrix modelling

Summary of vital parameters of *P. arachnoides* life history traits used in matrix modelling:

A Lefkovich (1965) stage class projection matrix to model the finite growth rate, matrix sensitivities and elasticities of *P. arachnoides* under a post-breeding scenario (sensu Caswell, 2001) was produced. In a Lefkovich matrix there is no relationship between stage and age but rather all members within a stage are subject to the same survival, fecundity and transition rates (Crouse et al., 1987). Adult survival and fecundity parameters were estimated *in situ* using capture-mark-recapture (CMR) techniques (Walker et al, 2012b; see Chapter 4) and data from

captive individuals (Zwartepoorte, 2003; Pedrono & Smith, in press), sub-adult, juvenile, hatchling and survival parameters were estimated from surrogate species due to a lack of available field data (Table 4).

Following Caswell (2001), a stage class projection matrix was produced in which each of the following were calculated: the reproductive rate (F_i), probabilities of surviving and growing to the next stage (G_i) and surviving and remaining in the same stage (P_i), based on the conceptual life history shown in Figure 13. The probabilities P_i and G_i were estimated from the survival probability of an individual in stage i (σ_i), probability of graduation to the next stage, given survival (γ_i) and duration in the stage (T_i) (Caswell, 2001):

equation 1.

$$G_i = \sigma_i \gamma_i$$

equation 2.

$$P_i = \sigma_i (1 - \gamma_i)$$

equation 3.

$$\gamma_i = \frac{\left(\frac{\sigma_i}{\lambda}\right)^{T_i} - \left(\frac{\sigma_i}{\lambda}\right)^{T_i-1}}{\left(\frac{\sigma_i}{\lambda}\right)^{T_i-1}}$$

As the value of γ_i in equation 3 was dependent on λ (population growth) the iterative approach of Caswell (2001) was used to produce a matrix which converged to have survival elements compatible with its own eigenvalues. The resulting stage class projection matrix took the following form:

$$\begin{pmatrix} P_1 & F_2 & F_3 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix}$$

The matrix analysis was conducted in program R (version 2.13.1) using the package Popbio. The dominant eigenvalue (λ) was established representing the finite rate of growth (Caswell, 2001). If $\lambda > 1$, the population is growing, if $\lambda < 1$, the population is declining. The rate of decline can be estimated as $1 - \lambda$. Sensitivity and elasticity analyses were also undertaken to test the impact and dependence of the population growth to variation in the matrix elements. Sensitivity examines the effect of a small incremental change, while elasticity examines the effect of a proportionate change (Caswell, 2001). The value of the right eigenvector of the matrix was calculated in order to establish the expected, stable state distribution of the spider tortoise population.

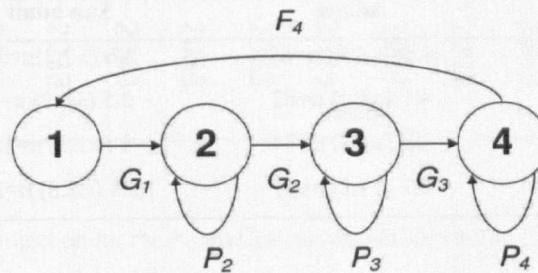


Figure 13: Life-history diagram of *P. arachnoides*. Where G_i = annual probability of surviving and recruiting into the next size class, P_i = annual probability of surviving and staying within the same size-class and F_i represents the annual production rate of female offspring per adult female.

Leslie matrix population projection model for *P. arachnoides*

Population dynamics was modelled using a stage based, linear, time-invariant, matrix model with a one year projection interval. The goal of the population modelling was to quantify the population growth rate under a regime of habitat deterioration, using field data detailing tortoise population density collected in 2003. Actual population densities for 2009, 2010 and 2011 were then compared against the projected population density over time for the next 200 years.

Results

Classified images had an overall accuracy of 86%. Reduction in vegetation cover equates to 7% within the c. 37.7km² study area between 2003 and 2009 (Fig. 12b), representing an annual mean reduction in vegetation cover of 1.2% yr⁻¹. Mean vegetation cover within the 15 individual 1 ha quadrats has declined from 45.1% (± 23.9) to 38.8% (± 20.7) (paired *t*-test; *P*=0.093); representing a mean loss of habitat of 0.9% yr⁻¹.

Table 5: Mean density of *P. arachnoides* for the three life stage classes across the 15 1 ha. survey quadrats within the coastal dry forests of Anakao for 2003, 2009, 2010 and 2011.

Year	Mean density of tortoises per ha. and total density across 15 survey quadrats			
	All life stages	Adults	Sub adult	Juvenile
2003	7.4 (± 6.8) n=111	4.6 (± 4.9) n=69	2.6 (± 2.2) n=39	0.1 (± 0.4) n=2
2009	5.9 (± 5.6) n=88	4.1 (± 4.6) n=62	0.5 (± 0.9) n=8	1.2 (± 1.9) n=18
2010	7 (± 5.8) n=105	4.9 (± 3.4) n=74	1 (± 1.3) n=15	1 (± 1.3) n=15
2011	6.6 (± 5.9) n=91	4.1 (± 3.2) n=51	2.1 (± 2.8) n=28	0.4 (± 0.7) n=5

Mean tortoises density has dropped from 7.4 (± 6.8) per ha during 2003 to 6.6 (± 5.9) per ha in 2011, with the greatest fluctuations in density between 2003 and 2009 equating to 20.3% during this six year period (Table 5; Fig. 14). There is an overall linear decline of 10.8% in mean population density over the eight years (2003-2011) (Table 5; Fig. 14), representing an annual mean decline of c. 1.4%. However, there is no significant drop in population density as a whole or within the three age classes (Table 6).

The dominant eigenvalue of the matrix is $\lambda = 0.986$; inferring a mean decline of c. 1.4% a year. Sensitivity and elasticity analyses show that adult survival (P_4) has the greatest contributing

effect to λ (Table 7). The values of the right eigenvectors suggest that the size-class distribution of spider tortoises can be expected to settle at the following ratio: eggs 0.27, juveniles 0.33,

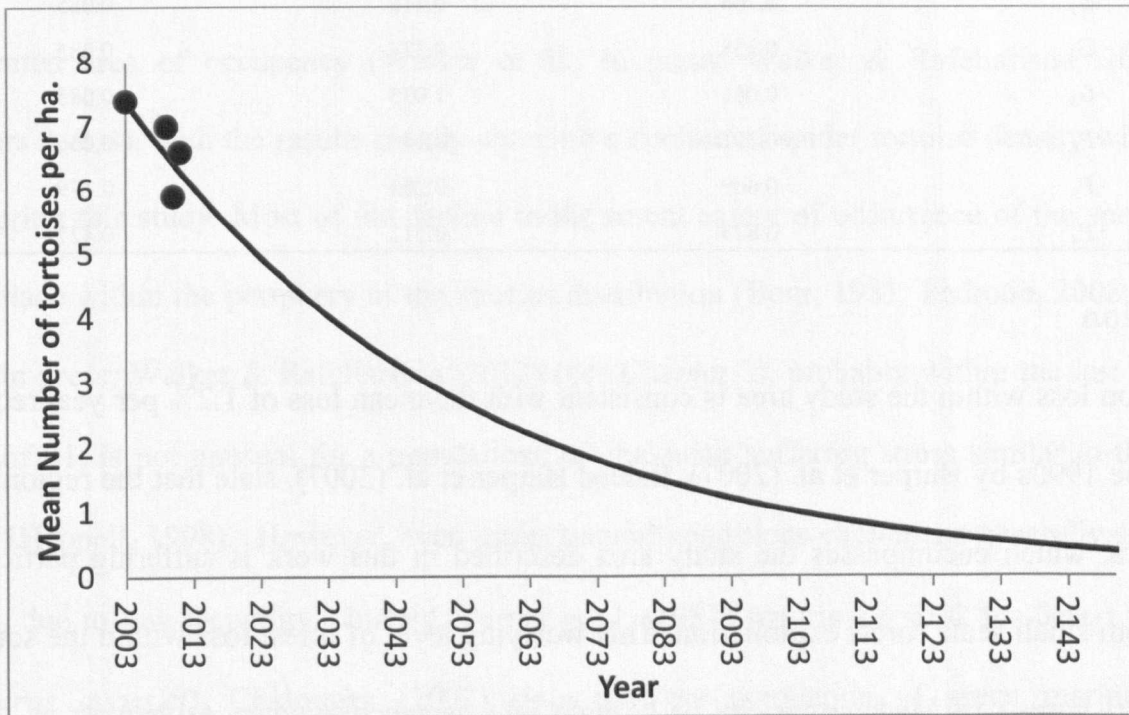


Figure 14: Results of the decline projection for the *P. arachnoides* population within the coastal dry forests of the Anakao region. The solid line represents the projected decline through to the year 2150. The dots represent the true mean population density values for the tortoise population for years 2003, 2009, 2010 and 2011.

Table 6: Results of regression analysis of *P. arachnoides* age class verses year (2003, 2009, 2010 and 2011).

Age class	All life stages	Adults	Sub adult	Juvenile
P value – regression analysis	0.461	0.775	0.434	0.465

subadults 0.27, and adults 0.13. The population projection of the matrix predicts a decline for the species (Fig. 14) with a density of less than <0.5 individuals per ha to occur at around 2182, in 170 years' time if the current vital rates remain unchanged.

Table 7: Stage-class projection matrix elements for *P. arachnoides* and associated sensitivities and elasticities.

Matrix Element	Value	Sensitivity	Elasticity
F_4	2.057	0.041	0.085
G_1	0.706	0.118	0.085
G_2	0.258	0.323	0.085
G_3	0.081	1.035	0.085
P_2	0.391	0.140	0.056
P_3	0.669	0.263	0.179
P_4	0.823	0.512	0.427

Discussion

Vegetation loss within the study area is consistent with the mean loss of 1.2% per year recorded during the 1990s by Harper et al. (2007). Indeed Harper et al. (2007), state that the region south of Toliara, which encompasses the study area described in this work is suffering particularly badly from small scale forest exploitation. This worrying level of forest loss within the southern coastal dry forests of Madagascar can be brought into perspective when Archard et al. (2002) predict that mean forest loss within Africa was only 0.4% per year, almost a third of what is being experienced within southwest coastal Madagascar. If vegetation loss is to be projected into the future based on a year on year decline of 1.2% an end point of complete habitat loss will be reached in approximately 83 years' time. However, despite the probable and gradual increase in degradation to the habitat over time, a complete loss of vegetation cover will probably not take place, as the drivers forcing the loss, such as charcoal production are somewhat selective in the species targeted, whereby unsuitable species will be left and invasive nonnative species will probably proliferate. As local environmental degradation increase with time and as possible land productivity issues develop, the small scale agricultural strategies currently employed within the region may change and adapt. However, how any of this long term habitat alteration effects the

long term survival of the spider tortoises and the species' ability, if any, to adapt is as yet unknown.

This study site is within the core of the range of what is now considered to be a fragmented area of occupancy (Walker et al., in press; Walker & Rafeliasoa, 2012; see Chapters 3 & 4), with the results clearly showing a decline of spider tortoise density within this area during this study. Most of the decline in the present extent of occurrence of the species has taken place within the periphery of the species distribution (Bour, 1981; Pedrono, 2008; Walker et al. (in press; Walker & Rafeliasoa, 2012) (see Chapter 2), probably within the last century. The λ of <1 , is not unusual for a populations of chelonian suffering stress similar to the study cohort (Heppell, 1998). However, even under natural conditions chelonians generally support a low λ , due to low fecundity. Indeed, Turner et al. (1987) reports $\lambda = 1.02$ for desert tortoises (*Gopherus agassizi*), Chaloupka (2002) state that the population of green marine turtles (*Chelonia mydas*) they studied in Australia supports $\lambda = 1.00$ and even species with rates of greater fecundity and shorter life cycles such as the common mud turtle (*Kinosternon subrubrum*) support low population multiplication rates (i.e. Frazer et al., 1991; $\lambda = 1.07$).

Although chelonians make excellent models for studies of life history strategies due to their longevity (Hellgren et al., 2000), obtaining sufficiently robust life history and demographic data can be problematic for threatened species, which often due to a lack of research support little biological and ecological data (Heppell et al., 2000; Engler et al., 2004). Pike et al., (2008) show that most survival probabilities for juvenile reptiles are underestimates due to the cryptic nature of these species almost always giving artificially low numbers for these life stages during CMR studies. This is true of *P. arachnoides* where capture rates during limited field studies (three visits over three years) result in almost nothing being known about the early life stages

(Walker et al., 2012b; see Chapter 4). Because of this, the model in this study incorporated an adjusted surrogate figure developed by Pike et al., (2008) for juvenile survival probability; data from a similar sized dry forest species for the sub-adult class survival probability (Loehr, 2010) and data from a sympatric species for egg survival probability (Table 4) for the model described in this work. The adult reproductive rate is open to conjecture, as few laying tortoises have ever been encountered in the wild and our data is based on reproductive rates of captive spider tortoises (Zwartepoorte, 2003; Pedrono & Smith, in press; Ogle pers comms). However, the surrogate data can be viewed with confidence as actual population size between 2003-2011 is consistent with modelled population size (Fig. 14).

Tortoise species are woefully under-represented within population modelling studies (Hellgren et al., 2000), particularly those which investigate the effects of anthropogenic pressures on a population. Such studies become all the more important from a species conservation perspective when one considers that one of the few studies investigating the effects of habitat fragmentation on forests tortoises *Chelonidis carbonaria* showed altered age structure, population density and growth rates (Aponte et al., 2003). The use of proportional elasticity and sensitivity analysis of demographic rates within a population (Mills et al., 1999) gives conservation practitioners guidance as to where to focus conservation effort. Adult survival is the most critical element in the calculation of λ for this population; a finding typical of long lived taxa such as chelonians (Pike et al., 2008). Management strategies to control habitat loss, through reducing fuel wood consumption, livestock grazing and collection of tortoises by local communities, particularly within protected areas, will reduce adult tortoise mortality, as well as other life stages, thus improving survival status. However, effectively implementing such

strategies would be difficult on account of the socio-economic and cultural situation in southern Madagascar (Gardner, 2011).

Quantifying the exact effects of vegetation loss on this species is very difficult due to the lack of suitable control sites supporting tortoises and not being subjected to anthropogenic habitat loss. Even the protected areas within the range of *P. arachnoides* are subjected to moderate amounts of disturbance from livestock herding, fuel wood removal and in some cases tortoise collection (Pedrono, 2008). The matrix population projection model predicts, what is considered a probable minimal viable population density within our study area to occur around the year 2182. There is generally a lack of available empirical data from home ranging studies allowing detailed knowledge of minimum population viability densities for small dry forest tortoises. However, a week long, small scale, preliminary study suggests that spider tortoises within our study area moved on average 47.85m (SE \pm 8.94) per 52 hour sampling period (Currylow, unpublished data). Therefore, it can be considered that a density of <0.5 animals per ha. would probably be enough to significantly affect the reproductive function of a very small species within a taxon that generally uses small home ranges (Morrow et al., 2001). Most population viability work for chelonians centres on desert tortoises *G. agassizii*, whereby Berry (1997) report that a minimal viable population size of 0.4 ha. within a protected area of 1,300 km² is required to allow for long term viability within a tortoise population.

When one considers the decline in comparison to IUCN categories, these results amount to a population declining by 1.4% annually. Unabated, this represents a 35% decline in population size during one generation (as based on IUCN criteria) and probable functional extinction within three generations. This decline can be attributed to habitat loss and if extrapolated across the species whole range, infers the species meets the criteria for Critically

Endangered status under criterion A4a (IUCN, 2001). Given that most of the rest of the remaining area of occupancy of *P. arachnoides* is probably not as densely populated as our study area (i.e. mean range wide density 2.3 tortoises per ha. Walker & Rafeliasoa, 2012) and that in some areas the species is exploited as a source of bush meat (Walker, 2010) or collected to fuel the illegal international pet trade (Walker et al., 2004), these populations elsewhere could become non viable sooner than the study population. It is likely that spider tortoise will suffer some degree of extinction debt, whereby many non reproductively viable populations of adult chelonians persist at low numbers within fragmented or degraded habitat (Doak et al., 1994; Berry, 1997). *P. arachnoides* appears to have a heavy association with vegetation cover (Walker et al., 2012a), however 2.5% of a population within this study site were recorded within quadrats supporting <10% vegetation cover during a separate study (i.e. Walker et al., 2007). Therefore it is plausible that a small, relic, nonviable population of adult animals of this species may persist long after the species becomes reproductively non viable, due to the potential longevity of the species; a factor not represented by the matrix model.

Projection population matrix modelling can only use the best, current, available data detailing the life history and mean survival for a species or population under the current or known conditions to predicted population dynamics into the future. Despite high levels of uncertainties it may be possible to improve model robustness through the use of a vortex parametric matrix method model (Lacy, 2000) as opposed to matrix modelling. The vortex technique allows the parameters of uncertainties within the data to be taken into consideration for data imputed into the model (i.e. 95% confidence limits). However, the greatest drawback to Vortex methods are that the model asks for data typically unavailable in conservation studies such as skewed sex ratios (Fieberg & Ellner, 2001). In the case of this study species, it would be

difficult to predict any synergistic effect of vegetation loss and population decline and if indeed vegetation loss will continue at the same rates and what effects this will have on the study species. It is unlikely that such a long lived species, with such low reproductive potential can adapt and display any form of resilience under such conditions. However, when trying to model the behaviour of a population facing anthropogenically induced impacts, one needs to consider the potential for the constantly changing dynamics of these impacts as a result changes in human behaviour. In the case of this study species and the local habitat, rates of vegetation loss could drastically change over relatively short periods of time as a result in changes in technology available to the local human populous. Tortoise mortality could increase as a result of addition threats not currently facing the species, such as poaching or introduction of invasive predatory species.

These current results emphasise the need for improved forest conservation efforts in southern Madagascar and the need for improved protected area management within the current and newly proposed protected areas within the region (Rabearivony et al., 2010; Gardner, 2011), to control the currently unsustainable exploitation of local forest resources. This unsustainable exploitation highlights the link between poverty elevation, social development and biodiversity conservation within southern Madagascar. Therefore, effective conservation strategies need to incorporate local communities and integrate poverty alleviation strategies if they are to be effective.

Chapter 6: Discussion

Clearly wild populations of the spider tortoise are in decline and the species is facing serious threats to its conservation and long term survival. In terms of more recent positive moves focusing conservation effort towards spider tortoises, the species' conservation status was assessed during 2008, by a working group of Madagascar tortoise species' experts. As a result, it was decided the species should be up listed from Vulnerable to Critically Endangered on the IUCN Red List. The species met the criteria used to classify the status of Critically Endangered based on habitat loss and exploitation (Leuteritz & Walker, 2008). However this assessment was based on population data of limited spatial resolution, or data derived from grey literature (Randriamahazo et al., 2007), or anecdotal evidence suggesting high rates of exploitation and finally used out of date published habitat contraction data (Harper et al., 2007).

It was not till the completion of the study documented within this thesis that we now have up to date, quantitative, empirical, peer reviewed results to suggest the species is suffering conservation threats such as sustained loss of habitat at $1.2\% \text{ yr}^{-1}$ between 2003 and 2011, within the core of its range; a rate that is consistent with forest loss within the southern dry forests between 1990 and 2000 (Harper et al., 2007). This amounts to a c. 30% reduction in habitat in one generation (as described by IUCN, 2001; IUCN Standards and Petitions Subcommittee, 2010). Therefore, predicted habitat loss for the species appears to meet the criteria for Critically Endangered under criterion A4c (90% habitat loss in three generations). This habitat loss is having a direct effect on population growth through low recruitment as demonstrated by the results of the population matrix modelling study for the population of tortoises in the Anakao region. Currently, this population, in the core of the spider tortoise's current range, is declining by c. 1.4% annually. Unabated, this represents a 35% decline in

population size during one generation and probable functional extinction within three generations. This decline can be directly attributed to habitat loss and if extrapolated across the species' whole range, infers the species meets the criteria for Critically Endangered status under criterion A4a (IUCN, 2001). Habitat loss has been a critical factor governing the conservation status of many of the world's Critically Endangered Chelonians. Kuchling & Bloxam (1988) and Bloxam et al. (1996) describe how *Pyxis planicauda* within the Menabe region of Madagascar has undoubtedly suffered as a result of loss of its native dry deciduous forest habitat, with the species now confined to what is thought to be approximately 69,000 ha. (Young et al., 2008). Meanwhile habitat loss is through to be a significant factor effecting the long term survival of c. 50% of the world's chelonians (Rhodin et al., 2011).

There is no available quantitative data detailing the human exploitation rates for *P. arachnoides*, so it is still difficult to establish if the species meets the IUCN criteria for Critically Endangered under criterion A4d. This criterion was awarded during the 2008 Red List assessment but was based on anecdotal information. The c. 71% decline from extent of occurrence (Bour, 1981; Pedrono, 2008) to current area of occupancy (Walker et al., in press) suggest a reduction in population, however this reduction in range and probable population size is difficult to quantify due to the differing measures used. However, rapid range decline is often a precursor for extinction of a species (Channell & Lomolino, 2001; Gaston & Fuller, 2009), with numerous historical examples of species becoming rapidly rarer through declining range and eventually extinction. The north American pigeon *Ectopistes migratorius* is one such classic example, whereby the species suffered rapid range decline as a result of human predation and habitat loss during the early 20th century, cumulating in extinction by 1914 (Ellsworth & McComb, 2003). The literature documents the decline in range of many endemic island species

similar to *P. arachnoides*, as a result in anthropogenic pressure. For example Fisher & Ineich (2012) carried out an extensive literature search documenting the declines and subsequent extinction of the cryptic, Hawaiian skink *Emoia impar*, during the early 1900s. Meanwhile, Gerlach's (2004) interpretation of the crude, historical accounts of the demise of the tortoise *Cylindrapis borbonica* on Reunion highlights the rapid range contraction prior to the demise of the species over an approximately 200 year period in the 1600s and 1700s.

Harper et al., (2007), predict that many of the locally endemic species inhabiting the diverse, southern, coastal dry forests within this region maybe living on 'borrowed time' given the probable lag-time of species extinction following habitat destruction (Brooks et al., 1999; Cowlshaw, 1999). The results of this study emphasise the need for increasing forest conservation efforts in southern Madagascar, an area which has historically been ignored by conservation policy (Gardner, 2011). In simplistic terms, there is a need for improved protected area management within the current and newly proposed protected areas within the region (Rabearivony et al., 2010). Indeed, the spider tortoise, as one of the more charismatic vertebrate species within the region could be used as a flagship species for the region and habitat. The use of the spider tortoise to anchor a habitat wide conservation campaign by conservation practitioners through the promotion of the tortoise (Simberlof, 1998) and therefore having wider ranging impacts for multiple species at the ecosystem and habitat level is a possibility.

The new regional protected area structure can go some way to facilitate the conservation of the 73.5% of the current area of occupancy of the species that falls within these areas. However, complete protection within these zones through responsible management is hard to guarantee. With the exception of the two National Parks (Mikea Forest and Tsimanampesotse) and Cap Sainte Marie Special Reserve, the protected areas that this species inhabits, are

currently, or are proposed as, IUCN category III, V or VI multiple-use protected areas (PAs). These PAs will be, or are currently, co-managed by local community associations and aim to simultaneously conserve biodiversity while promoting the sustainable use of natural resources to alleviate poverty and for local development (Gardner et al., 2008; Gardner, 2011). They also place emphasis on the avoidance of negative impacts on local communities due to resource use restrictions. As a result, in reality, these PAs will be zoned to permit continued forest resource use through much of their area, and are likely to suffer continuing habitat degradation (Gardner, 2009; 2011) with potential negative implications for tortoise populations. Further, surveillance and control within these PAs will largely be undertaken by local communities, with the result that local consumption of tortoises, in regions where this takes place can be expected to continue unless local agreement can be reached to cease the practice. Such agreements may be difficult to reach, given the poverty and food insecurity (Gardner, 2011) of these communities. It is therefore simplistic to assume that the creation of protected areas alone will be sufficient to ensure the viability of spider tortoise populations within such sites. However, if future conservation strategies are to work and habitat becomes more effectively protected and poaching reduced there is no reason to suggest that populations of this dwindling species cannot recover to some extent. For example, Gerlach (2008) reports that populations of long lived, *K* strategists such as chelonians can recover given adequate protection from drivers which induce unnatural levels of mortality. For example, the rapid recovery of the Critically Endangered fresh water turtle *Pelusios subniger parietalis* on Frigate Island in the Seychelles, came about through improvements in habitat management whereby the population increased by c. 90% in 30 years. The Aldabra giant tortoise (*Dipsochelys dussumieri*) has recovered from numbers as low as a 1,000 in the late 1800s as a result of harvesting, to current levels of 100,000 in response to

management regimes to control invasive species such as goats and human harvesting (Gerlach, 2004).

A number of large scale mining operations are proposed within the range of *P. arachnoides* in the near future. Spider tortoises are protected under Malagasy law (Pedrono, 2008). However, there is no set policy or guidelines in place to mitigate potential or actual impact as a result of operations undertaken under by the National Mining Code, to either endangered species such as tortoises or other species or habitats. Mining operations, particularly in developing countries where environmental impact assessment is sometimes poorly enforced, have often contributed to a negative perception by the general public and conservation community of mining companies (Labonne, 1999; Veiga & Hinton, 2002). The government of Madagascar, the international mining companies engaged in proposed mineral extraction projects and conservation NGOs, need to work in partnership during the planning stage of the proposed operations and plan and implement effective environmental mitigation strategies for this and other threatened species occurring within the region.

Two main mitigation strategies are available and have been used in similar situations; the first being a thorough and well-coordinated tortoise translocation program, whereby animals are collected from sites where populations face threats from mineral extraction impacts and are then moved to protected areas within the taxon's natural range (Burke, 1991; Field et al., 2007). Translocation has been accomplished reasonably effectively in North America for some of the *Gopherus* species of tortoises (Berry, 1986; Field et al., 2007). However, mortality can be high in certain circumstances, due to stress or spread of disease between different populations (Berry, 1986). The preservation of genetic diversity is important when managing the conservation of endemic species with restricted ranges (Booy et al., 2000) and translocation projects also run the

risk of causing unwanted genetic mixing (Dodd & Seigel, 1991). In the case of spider tortoises the effects of population fragmentation and the need to preserve the genetic and morphological characteristics of the three subspecies and populations in the zones of intergradation require careful consideration before translocation attempts. A successful translocation project would also depend on the existence of translocation areas in which the threats (i.e. collection, local consumption and habitat destruction) that have led to local extinctions through much of the spider tortoise range could be successfully reduced.

The second potential form of mitigation strategy is for mining companies, in consultation with the conservation sector, to identify and gazette as protected areas, proposed extraction sites which support good populations of tortoises. The sites could be managed by the mining companies with technical support from conservation NGOs. The Venetia Limpopo Nature Reserve in South Africa, initially established by the De Beers mining company, then later incorporated into the Vhembe Dongola National Park, provides an example of such partnerships (Yakovleva, 2005). This strategy has often been seen as an easy way of generating positive publicity for companies operating in a sector with an actual or perceived poor environmental record (Yakovleva, 2005). On account of the region's unique biological diversity (Seddon et al., 2000) and the attention and focus from the international conservation community, it is important that any mineral extraction be undertaken with a full and rigorous environmental mitigation strategy. Currently the lack of infrastructure and political instability are limiting factors restricting mineral exploitation in southwest Madagascar in the imminent future (Sarrasin, 2006), thus allowing time for full mitigation and impact strategies to be established.

If managed correctly the proposed mineral extraction could bring much needed economic development to the impoverished southwest coastal region of Madagascar. It is inevitable that

forest resource use and subsequent habitat degradation will continue in the region because of the multiple-use nature of most of the new protected areas and the proposed mineral extraction. However, with careful planning, management and dialogue between the mineral extraction companies, local communities, government and conservation practitioners, this impact can be mitigated and controlled to some extent. Almost all of the spider tortoises' current range will come under some form of tenure by mineral extraction companies, Madagascar National Parks or the communities who will manage the new multiple use protected areas.

The implementation of large scale community sensitization programs, such as environmental education, community outreach work and tortoise poaching enforcement work is essential if conservation of this threatened species is to work in this marginalised region. It is suspected that most of the poaching of tortoises for the pet trade is undertaken by gangs from outside of the region and will therefore be more difficult to address (WWF, 2010). WWF has had a limited amount of success in intercepting poaching gangs and poached tortoises in the region (WWF, 2010). A number of small scale conservation projects are succeeding in the region (Rafeliasoa et al., 2010). For example, a unique project is underway within the range of *P. a. brygooi* to provide local communities with reproductive health and family planning (Mohan, 2009; Harris et al., 2012) alleviating local population pressure on fuel wood in tortoise habitat. These projects, however, are limited in their geographical scope and most areas within the region lack any kind of initiative to draw communities away from the heavy reliance and over exploitation of natural resources that result in habitat loss.

This study acts as a useful model to describe the most effective methods for establishing the current population status of threatened, dry forest chelonian species. Indeed as a result of this work we now have one of the greatest understandings of the conservation status of any of the

world's small dry forest chelonians. The next step is to implement sound, workable, community based conservation efforts. There are a number of examples of how improving the knowledge of a species' status has positively contributed to the development of sustainable conservation management policies within developing regions of the world. For example, the greater understanding obtained from robust field data directed at the small, Critically Endangered, Egyptian tortoise; *Testudo kleinmanni* (Perälä, 2003), developed during the last decade (Baha et al., 2003; Attum et al. 2007a) has led to the implementation of effective community based conservation programs for the species through livelihood generation directing local people away from poaching (Attum et al. 2007b; Attum et al. 2008; Rhodin et al., 2011). Extensive work on establishing the status of other similar species, however less threatened, such as the five *Homopus* tortoise species in South Africa (Loehr, 2002; 2005; 2006; 2008), have led to more stringent conservation measures, allowing the species to enjoy relative sustainable conservation management. Unlike many species of tortoise, particularly within this region this species still supports healthy populations and with the current, active management of the species in place it is hoped that this species will be protected from many of the drivers which push many other less carefully monitored and managed and subsequently more threatened species of chelonian to the verge of extinction (Loehr, 2008).

There are a number of other Critically Endangered species of small dry forest tortoises for which this research could be used and systematically applied, to rigorously evaluate their status. Currently it is thought that the Burmese star tortoise *Geochelone platynota* is on the verge of extinction, with its range now thought to be very fragmented, with possibly just a small number of very small populations of variable numbers of individuals remaining (Platt et al., 2003; Rhodin et al., 2011). Political constraints and high levels of poverty have led to a lack of

research and are subsequently thought to be the main drivers of the conservation threats facing this species (Platt et al., 2003). Similarly, the Endangered geometric tortoise *Psammabates geometricus* of South Africa which now occupies one of the narrowest ranges of any tortoise species of just 22km² (Rhodin et al., 2011) would benefit from being subjected to population projection modelling to assess the exact vulnerability of this species in its current status. Indeed this model or similar in depth studies into the status of a species could well be applied to the 98 species of chelonian listed as Endangered or Critically Endangered (van Dijk et al., 2011), with an emphasis place on the species which have been classified without the aid of sufficient amounts of empirical, peer reviewed published data. In this case the 11 species listed as Data Deficient on the IUCN Red List for Threatened Species should undergo assessment using this model.

The reliance upon grey literature and personal communications for assessing the threat to many species and there subsequent assignment to an IUCN Red Listing category is most likely due to a lack of interest or indeed available funding to allow the scientific community to collect these necessary data, particularly for less charismatic species which have traditionally attracted less interest and funding (Garnet et al., 2003). The Red Listing process is far from being a panacea for assessing the intrinsic threat of extinction facing a particular species. Indeed, even with the availability of adequate data, assessing risk of extinction using a standard set of criteria for every species is intrinsically constrained and limited by species' differences in life histories, population dynamics, threats faced and in available information and understanding about their numbers and circumstances (Mrosovsky & Godfrey, 2008). In the case of the spider tortoise the species' listing in 2008 as Critically Endangered on the IUCN Red List for Threatened Species based on data of limited spatial resolution and anecdotal information, served a purpose, whereby

the species gained conservation attention. As a result, adequate funds and resources could be directed at the species over the next four years to rigorously test the status of the species and subsequently present novel, up to date, empirical peer reviewed data (Walker, 2010; Walker et al., 2012a; 2012b; 2012c), in this case proving that the designation was indeed correct based upon the criteria outlined by IUCN (IUCN Standards and Petitions Subcommittee, 2010). Indeed, as a condition of the use of the best available data (which in many cases maybe grey literature or antidotal information) a condition could be placed on the designation of a particular species, whereby the respective IUCN specialist group interested in the species have five years to provide strong empirical, peer reviewed data to support the classification. Therefore, by assigning this temporary conditional designation of high conservation importance to a particular species (i.e. Endangered or Critically Endangered) this acknowledgment of conservation concern can then be used as leverage to secure much needed conservation funds to allow work to be carried out to rigorously assess the status of the species in question. Conversely, if further studies prove that the species' is not as threatened as first suspected then the species can be moved to a lower category as appropriate according to the IUCN Red Listing criteria.

Acknowledgments

This work was financially supported through conservation grants from the following organisations; EAZA/Shell Shock Turtle Conservation Fund, Turtle Survival Alliance, Royal Geographical Society, British Chelonia Group, Mohamed Bin Zayed Species Conservation Fund, Leicester Tortoise Society, Chelonian Research Foundation and further funds were supplied by the Open University Access to Learning Fund.

Logistical support and assistance with field work was provided by Inge Smith, Solonombana Vitantsoa, Alice Ramsay, Harrison Randrianasolo, Hery Rasolohery, Al Harris, Andy Woods-Ballard, Charley Rix, Sarah de Mobray, Mima Stancombe, Mike Cummings, Matt Perkins, Riana Rakotondrainy, Eddie Louis, Brain Horne, Julian Bruchard, Richard Razafimanatsoa, Jean Caude Rakotoniaina, Anjara Andriamanalina, Athanase Maminirina, Gervais Sylvestre Rakotoarivelo and Madagascar National Parks and Blue Ventures Conservation. Inge Smith provided some photographs.

This work was partnered by the Madagascar Institut pour la Conservations des Ecosystèmes Tropicaux (MICET), Ministère de l'Environnement et de Forêts and the University of Antananarivo. Landsat TM derived shapefiles comprising forest cover and land use data was generously donated by Conservation International and WWF Madagascar. The GeoEye Foundation supplied high resolution remotely sensed IKONOS 2 imagery as a part of a GIS data grant. Project supervision was provided by Mike Gillman, Justin Gerlach and Mandy Dyson. Ross Sinclair, Nathan Whitmore, Sarah Hamylton and Luca Luselli provided helpful advice on some technical aspects of distance sampling, matrix modelling, Cormack-Jolly-Seber models and GIS/remote sensing respectively. Unpublished information on isolated tortoise sightings was provided by Rick Hudson and tortoise fecundity data was supplied by Jutta Hammer and Michael

Ogle. Editorial comments and suggested improvements of drafts of manuscripts contained within this thesis were provided by Alice Ramsay, Justin Gerlach, Mike Gillman, Mandy Dyson, Michael Ogle, Robert Jehle, Brad Moon, Richard Lehtinen, Miguel Pedrono, Craig Turner, Martin Fisher, Jonathan Stober, Christina Castellano, Gad Perry, Anders Rhodin, Sylvain Ursenbacher, Brian Halstead, Niqui Cummings, Andrea Currylow, Chris Barrett and a large number of anonymous reviewers. I am in debt to Charlie Gardner for not only reviewing manuscripts contained within this thesis, but for also providing invaluable information through long discussions over beer on the wider biodiversity conservation issues within southern Madagascar. Many thanks to Rick Hudson and the Turtle Survival Alliance, for their support to this project from the outset and the conservation of *Pyxis arachnoides* in general. This work would have been impossible without the truly herculean efforts of Tsilavo Rafeliasoa through support and assistance in the field; truly one of the future ambassadors for biodiversity conservation management in Madagascar. There was constant and generous logistical support provided by Eddie Louis and the Madagascar Biodiversity Partnership throughout the project which is greatly appreciated. A large thank you to the coastal forest communities of south west Madagascar for granting access to community owned land. This thesis was pieced together over a number of years during spare moments, hours or days, mostly whilst concurrently undertaking contract ecological surveying work in various places in the world. I'm therefore indebted to the dozens of people or organisations who supplied me with internet connections and electricity; either knowingly or unknowingly. In addition to this, many beds for the night or patches of floors have been supplied or places to park my van by friends whilst in the UK, during a couple of slightly more nomadic years – I thank you all for hospitality and kindness. Finally, thanks to the

medical staff of Bangor General Hospital for eventually diagnosing and treating my field work induced malaria.

References

- Akin, J.A. (1998) Fourier series estimation of ground skink population density. *Copeia*, 2, 519–522.
- Altmann, J. (1974) Observational study of behaviour: sampling methods. *Behaviour*, 49, 227–267.
- Anadón, J.D., Giménez, A., Martínez, M., Martínez, J., Pérez, I. & Esteve, M.A. (2006) Factors determining the distribution of the spur-thighed tortoise *Testudo graeca* in south-east Spain: a hierarchical approach. *Ecography*, 29, 339–346.
- Anderson, D.R., Burnham, K.P., Lubow, B.C., Thomas, L., Corn, P.S., Medica, P.A. & Marlow R.W. (2001) Field Trials of Line Transect Methods Applied to Estimation of Desert Tortoise Abundance. *The Journal of Wildlife Management*, 65, 583-597.
- Anderson, D.R. & Pospahala, R.S. (1970) Correction of bias in belt transects of immobile objects. *Journal of Wildlife Management*, 34, 141–146.
- Andriamalala, G. & Gardner, C. J. (2010) L'utilisation du *dina* comme outil de gouvernance des ressources naturelles: leçons tirées de Velondriake, sud-ouest de Madagascar. *Tropical Conservation Science*, 3, 447-472.
- Aponte, C., Barreto G.R. & Terborgh, J. (2003) Consequences of habitat fragmentation on age structure and life history in a tortoise population. *Biotropica*, 35, 550-555.
-

- Archard, F., Eva, H.D., Stibig, H.J., Mayaux, P. Gallego, J. Richards, P. & Malingreau, J.P. (2002) Determination of deforestation rates of the world's humid tropical forests. *Science*, 297, 999–1002.
- Armstrong, D.G. (1972) Distribution of mammals in Colorado. *University of Kansas Publication of Natural History Monographs* 3, 415.
- Attum O, El Din MB, Baha El Din SM, Habinan S (2007b) Egyptian tortoise conservation: a community-based, field research program developed from a study on a captive population. *Zoo Biology* 26:397–406.
- Attum, O., Esawy, M.M., Farag W.E., Gad A.E., Baha El Din S.M., Kingsbury, B. (2007a) Returning them back to the wild: movement patterns of repatriated Egyptian tortoises, *Testudokleinmanni* Lortet, 1883 (Sauropsida: Testudinidae). *Zoology of the Middle East* 41:35–40.
- Attum, O., Rabea, B., Osman, S., Habinan, S., Baha El Din, S.M., Kingsbury, B. (2008) Conserving and studying tortoises: a local community visual-tracking or radio-tracking approach? *Journal of Arid Environments*, 72, 671–676.
- Baha El Din, S.M., Attum, O., Baha El Din, M. (2003) Status of *Testudo kleinmanni* and *T. wernerii* in Egypt. *Chelonian Conservation and Biology*. 4, 648–655.
- Baker, R.H. (1956) Mammals of Coahuila, Mexico. *University of Kansas Publication of Natural History Survey of North American Fauna*. 55, 416.
-

- Berry, K. (1997) The desert tortoise recovery plan: An ambitious effort to conserve biodiversity in the Mojave and Colorado deserts of the United States. In *Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles—an International Conference*. New York Turtle and Tortoise Society, 430-440.
- Berry, K.H. (1986) Desert tortoise (*Gopherus agassizii*) relocation: implications of social behavior and movements. *Herpetologica*, 42, 113–125.
- Bertolero, A., Oro, D. & Besnard, A. (2007) Assessing the efficacy of reintroduction programmes by modelling adult survival: the example of Hermann's tortoise. *Animal Conservation*, 10, 360-368.
- Best, L.B. (1981) Seasonal changes in detection of individual bird species. *Studies in Avian Biology*, 6, 252–261.
- Bjorndal, K.A., Bolten, A.B., & Chaloupka, M.Y. (2003) Survival probability estimates for immature green turtles *Chelonia mydas* in the Bahamas. *Marine Ecology Progress Series*, 252, 273–281.
- Bloxam, Q.M.C., Nody, J.P., Rabenjanahary, R.D. & Gibson, R. (1996) Estimating density and abundance of the Madagascar flat-tailed tortoise. *Dodo*, 32, 132–136.
- Bodin, Ö., Tengö, M., Norman, A., Lundberg, J., & Elmqvist, T. (2006) The value of small size: loss of forest patches and ecological thresholds in southern Madagascar. *Ecological Applications*, 16, 440–451.
-

- Bombi, P., Luiselli, L., & D'Amen, M. (2011) When the method for mapping species matters: defining priority areas for conservation of African freshwater turtles. *Diversity and Distributions*, 17, 581–592.
- Booy, G., Hendriks, R.J.J., Smulders, M.J.M., van Groenendael, J.M. & Vosman, B. (2000) Genetic diversity and the survival of populations. *Plant Biology*, 2, 379-395.
- Bour, R. (1981) Etude systématique du genre endémique Malagache *Pyxis* Bell, 1827 (Reptilia, Chelonii). *Bulletin Mensuel de la Société Linnéenne de Lyon*, 50, 154-176.
- Bour, R. (1984) Les tortues terrestres géantes des îles de l'Océan Indien Occidental: données géographiques, taxinomiques et phylogénétiques. *Studia Geologica Salmanticensia Volume Especial*. 1, 17-76.
- Bowen, B.W., Bass, A.L., Soares, L., Toonen, R.J. (2005) Conservation implications of complex population structure: lessons from the loggerhead turtle (*Caretta caretta*). *Molecular Ecology*, 14, 2389–2402.
- Brito, D. (2010) Overcoming the Linnean shortfall: data deficiency and biological survey priorities. *Basic Applied Ecology*, 11, 709-713.
- Brooks, T. M., Pimm, S.L. & Oyugi, J.O. (1999) Time lag between deforestation and bird extinction in tropical forest fragments. *Conservation Biology*, 13, 1140–1150.
- Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A.B., Gerlach, J., Hoffmann, J., Lamoreux, F.J., Mittermeier, C.J., Pilgrim J.D. & Rodrigues, A.S.L. (2006) Global Biodiversity Conservation Priorities. *Science*, 313, 58 – 61.
-

- Brown, J.H. & Lomolino, M.V. (1998) *Biogeography*. Sinauer Press Sunderland, Massachusetts, USA.
- Buckland S.T., Magurran A.E., Green R.E. & Fewster R.M. (2005) Monitoring change in biodiversity through composite indices. *Philosophical Transactions of the Royal Society*, 360, 243–254.
- Buckland, S.T. (1985) Perpendicular distance models for the line transect sampling. *Biometrics*, 41, 177-195.
- Buckland, S.T., Anderson, D.R., Burnham, K.P. & Laake, J.L. (2001) *Distance Sampling: Estimating Abundance of Biological Populations*. Chapman and Hall, London, UK.
- Burke, R.L. (1991) Relocations, repatriations, and translocations of amphibians and reptiles: taking a broader view. *Herpetologica*, 47, 350–357.
- Burnham, K.P., Anderson D.R. & Laake, J.L. (1980) Estimation of density from line transect sampling of biological populations. *Wildlife Monographs*, 72, 1–202.
- Caccone, A., Amato, G., Gratry, O.C., Behler, J & Powell, J.R. (1999) A Molecular Phylogeny of Four Endangered Madagascar Tortoises Based on MtDNA Sequences. *Molecular Phylogenetics & Evolution*, 12, 1-9.
- Cagle, F.R. (1939) A system of marking turtles for future identification. *Copeia*, 1939, 170-173.
- Casse, T., Milhøj, A., Ranaivoson, S. & Randriamanarivo, J.R. (2004) Causes of deforestation in southwestern Madagascar: what do we know? *Forest Policy & Economics*, 6, 33-48.
-

- Caswell, H. (2001) *Matrix Population Models: Construction, Analysis, and Interpretation*. 2nd ed. Sinauer Associates, Sunderland, Massachusetts, USA.
- Chaboud, C., Me´ral P.H., Andrianambinina, D. (2004) Le mode`le vertueux de l'e´cotourisme: mythe ou re´alite´? L'exemple d'Anakao et Ifaty-Mangily a`Madagascar. *Mondes le de´veloppement*, 32, 11–32.
- Chaloupka, M. (2002) Stochastic simulation modelling of southern Great Barrier Reef green turtle population dynamics. *Ecological Modelling*, 148, 79–109.
- Channell, R. & Lomolino, M.V. (2001) Dynamic biogeography and conservation of endangered species. *Nature*, 403, 84–86.
- Chen, T.H., Chang, H.C. & Lue, K.Y. (2009) Unregulated trade in turtle shells for Chinese traditional medicine in East and Southeast Asia: the case of Taiwan. *Chelonian Conservation and Biology*, 8, 11-18.
- Chiari, Y., Thomas, M., Pedrono, M. & Veites, D.R. (2005) Preliminary data on genetic differentiation within the Madagascar spider tortoise, *Pyxis arachnoides* (Bell, 1827). *Salamandra*, 41, 35-43.
- Coblentz, B.E. (1978) The effects of feral goats (*Capra hircus*) on island ecosystems. *Biological Conservation*, 13, 279-286.
- Coulson, T., Albon. S, Guinness. F, Pemberton. J, & Clutton-Brock, T. (1997) Population substructure, local density, and calf winter survival in red deer (*Cervus elaphus*). *Ecology*, 78, 852–863.
-

- Cowlshaw, G. (1999) Ecological and social determinants of spacing behaviour in desert baboon groups. *Behavioural Ecology & Sociobiology*, 45, 67-77.
- Crouse, D.T., Crowder, L.B., Caswell, H. (1987) A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology*, 68, 1412-1423.
- Dewar, R.E. (1984) Extinctions in Madagascar, In *Quaternary Extinctions: a prehistoric revolution*. (eds P.S. Martin, & R.G. Klein, R.G), pp. 574-593. University of Arizona Press, Tucson, Arizona, USA.
- Doak, D., Kareiva, P. & Klepetka, B. (1994) Modelling population viability for the desert tortoise in the western Mojave Desert. *Ecological Applications*, 4, 446-460.
- Dodd C.K & Seigel, R.A. (1991) Relocation, repatriation and translocation of amphibians and reptiles: are they conservation strategies that work? *Herpetologica*. 47, 336-350.
- Dodd, C. K., & Dreslik, M.J. (2008) Habitat disturbances differentially affect individual growth rates in a long-lived turtle. *Journal of Zoology*, 275, 18-25.
- Donque, G. (1972) The Climatology of Madagascar. In *Biogeography and Ecology of Madagascar* (eds R. Battistini & G. Richard-Vindard), pp. 87-144. Junk, The Hague, The Netherlands.
- Dupont, J.F. (1969) Recueil de documents pour servir à l'histoire de Rodrigues. *Mauritius Archives*, 10, 121.
-

- Ellsworth, J.W. & McComb, B.C. (2003) Potential effects of passenger pigeon flocks on the structure and composition of presettlement forests of eastern North America. *Conservation Biology*, 17, 1548-1558.
- Engler, R., Guisan, A., & Rechsteiner, L. (2004) An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology*, 41, 263-274.
- Fenn, M. (2003) The spiny forest ecoregion. In *The Natural History of Madagascar* (eds S.M. Goodman & J.P. Benstead), pp. 1525–1530. University of Chicago Press, Chicago, Illinois, USA.
- Fernández-Chacón, A., Bertolero, A., Amengual, A., Tavecchia, G., Homar, V. & Oro, D. (2011) Exploring the effects of climate change on the population dynamics of a Mediterranean tortoise. *Global Change Biology*, 17, 3075-3088.
- Fieberg, J. & Ellner, S.P. (2001) Stochastic matrix models for conservation and management: a comparative review of methods. *Ecology Letters*, 4, 244–266.
- Field, K.J., Tracy, C.R., Medicab, P.A., Marlowa, R.W. & Corn, P.S. (2007) Return to the wild: Translocation as a tool in conservation of the desert tortoise (*Gopherus agassizii*). *Biological Conservation*, 136, 232–245.
- Fisher, R.N. & Ineich, I. (2012) Cryptic extinction of a common Pacific lizard, *Emoia impar*, from the Hawaiian Islands (Squamata, Scincidae) *Oryx*, doi: 10.1017/S0030605310001778
-

- Fox, G. A. (1993) Life history evolution and demographic stochasticity. *Evolutionary Ecology*, 7, 1–14.
- Frazer, N.B., Gibbons, J.W. & Greene, J.L. (1991) Life history and demography of the common mud turtle *Kinosternon subrubrum* in South Carolina, USA. *Ecology*, 72, 2218–2231.
- Gardner, C. J. (2009) A review of the impacts of anthropogenic habitat change on terrestrial biodiversity in Madagascar: Implications for the design and management of new protected areas. *Malagasy Nature*, 2, 2–29.
- Gardner, C.J. (2011) IUCN management categories fail to represent new, multiple use protected areas in Madagascar. *Oryx*, 44, 336–346.
- Gardner, C.J., Ferguson, B., Rebara, F., & Ratsifandrihamanana, A.N. (2008) Integrating traditional values and management regimes into Madagascar's expanded protected area system: the case of Ankodida. In *Protected Landscapes and Cultural and Spiritual Values* (ed J.M. Mallarach), pp. 92–103. IUCN, Kasperek Verlag, Heidelberg, Germany.
- Gardner, S. Baard, E.H.W. & Le Roux, N.J. (1999) Estimating the detection probability of the geometric tortoise. *South African Journal Wildlife Research*, 29, 62–71.
- Garnett, S.T., Crowley, G.M. & Balmford, A. (2003) The costs and effectiveness of funding the conservation of Australian threatened birds. *BioScience*, 53, pp 658–665.
- Gaston, K.J & Fuller, R.A. (2009) The size of species geographic ranges. *Journal of Applied Ecology*, 46, 1–9.
-

- Gaston, K.J. (1991) How large is a species' geographic range? *Oikos*, 61, 434–438.
- Gaston, K.J. (1994) Measuring geographic range sizes. *Ecography*, 17, 198–205.
- Gaston, K.J. (2003) *The Structure and Dynamics of Geographic Ranges*. Oxford University Press, Oxford, UK.
- Gautier, L., & Goodman, S.M.. (2003) Introduction to the Flora of Madagascar. In: Goodman, S.M. & Benstead, J.P. (Eds.). *The Natural History of Madagsacar*. University of Chicago Press, Chicago, USA.
- Gerlach, J (2004) *Giant Tortoises of the Indian Ocean: The Genus Dipsochelys inhabiting the Seychelles Islands and the Extinct Giants of Madagascar and the Mascarenes*. Chimiara publishers, Frankfurt, Germany.
- Gerlach, J (2008) Fragmentation and demography as causes of population decline in Seychelles freshwater turtles (Genus *Pelusios*). *Chelonian Conservation and Biology*, 7, 78-87.
- Gerlach, J. & Canning, K.L. (1998) Taxonomy of Indian Ocean giant tortoises (*Dipsochelys*). *Chelonian Conservation and Biology*, 3, 3-19
- Gerlach, J., Muir, C. & Richmond, D. (2006) The first substantiated case of trans-oceanic tortoise dispersal. *Journal of Natural History*, 40, 41-43.
- Germano, D. J. (1998) Scute and age determination of desert tortoises revisited. *Copeia*, 1998(2), 482-484.
-

- Glaw, F. & Vences, M. (1994) *A Field Guide to the Amphibians and Reptiles of Madagascar*. MoosDruck, Leverkusen & FARBO, Koln, Germany.
- Godfrey, M.H., & Godley, B.J. (2008) Seeing past the red: flawed IUCN global listings for sea turtles. *Endangered Species Research*, 6, 155-159.
- Goehring, D.M., Daily, G.C., Dasgupta, S. & Ehrlich, P.R. (2007) Range occupancy and endangerment: a test with a butterfly community. *The American Midland Naturalist*, 157, 106-120.
- Goodman, S. M. & Benstead, J.P. (2005) Updated estimates of biotic diversity and endemism for Madagascar. *Oryx*, 39, 73–78.
- Greenwood, J.J.D. (1996) Basic techniques. In *Ecological Census Techniques: a Handbook* (ed W.J. Sutherland), pp. 11-109. Cambridge University Press, Cambridge, UK.
- Griffith, B., Scott, J.M., Carpenter, J.W. & Reed, C. (1989) Translocation as a species conservation tool: status and strategy. *Science*, 245, 477-480.
- Gustafson, E.J., Murphy, N.L. & Crow, T.R. (2001) Using a GIS model to assess terrestrial salamander response to alternative forest management plans. *Journal of Environmental Management*, 63, 281–292.
- Hailey, A. & Coulson, I.M. (1999) Measurement of time budgets from continuous observation of thread-trailed tortoises (*Kinixys spekii*). *Herpetological Journal*, 9, 15-20.
-

- Hailey, A. & Willemsen, R.E. (2000) Population density and adult sex ratio of the tortoise *Testudo hermanni* in Greece: evidence for intrinsic population regulation. *Journal of Zoology*, 251, 325-338.
- Hailey, A. (2000) The effects of fire and mechanical habitat destruction on survival of the tortoise *Testudo hermanni* in northern Greece. *Biological Conservation*, 92, 321-333.
- Harper, G., Steininger, M., Tucker, C., Juhn, D. & Hawkins, F. (2007) Fifty years of deforestation and forest fragmentation in Madagascar. *Environmental Conservation*, 34, 325-333.
- Hellgren, E.C., Kazmaier, R.T., Ruthven, D.C. & Synatzske, D.R. (2000) Variation in tortoise life history: Demography of *Gopherus berlandieri*. *Ecology*, 81, 1297-1310.
- Heppell, S.S. (1998) Life-history theory and population model analysis to turtle conservation. *Copeia*, 1998, 367-375.
- Heppell, S.S., Caswell, H. & Crowder, L.B. (2000) Life histories and elasticity patterns: Perturbation analysis for species with minimal demographic data. *Ecology*, 81, 654-665.
- Hestbeck, J. B. (1995) Bias in transition-specific survival and movement probabilities estimated using capture-recapture data. *Journal of Applied Statistics*, 22, 737-750.
- Hoffmann, M., C. Hilton-Taylor and 172 other authors (2010) The impact of conservation of the status of the world's vertebrates. *Science*, 330, 1503-1509.
-

IUCN (2001) *IUCN Red List Categories and Criteria: Version 3.1*. IUCN Species Survival Commission. IUCN, Gland, Switzerland & Cambridge, UK.

IUCN (2012) *2012 IUCN Red List of threatened species v 2011.2*. <http://www.iucnredlist.org>. [accessed 10 April 2012].

IUCN Standards and Petitions Subcommittee (2010) *Guidelines for Using the IUCN Red List Categories and Criteria. Version 8.1*. IUCN Species Survival Commission. IUCN, Gland, Switzerland & Cambridge, UK.

Jathanna, D.N., Kumar, S. & Ullas Karanth, K. (2008) Measuring Indian giant squirrel *Ratufa indica* abundance in southern India using distance sampling. *Curent Science*, 95, 885-888.

Jesu, R. & Schimmenti, G. (1995) A preliminary study on the status of a population of Malagasy Spider tortoise *Pyxis arachnoides* Bell, 1927 from SW Madagascar. In: *International Congress of Chelonian Conservation*. (eds. B. Devaux, Gonfaron, France). 6th–10th. July 1995.

Kuchling, G. & Bloxam, Q.M.C. (1988) Field data on the Madagascan flat tailed tortoise *Pyxis (Acinixys) planicauda*. *Amphibia-Reptilia*, 9, 175–180.

La Caille, N.L. & Abbe D (1763) *Journal Historique du voyage fait au Cap de Bonne Esperance par feu M. l'Abbe de al Caille*. Guillyn, Paris, France.

Laake, P. (1978) An Evaluation of Synthetic Estimates of Employment. *Scandinavian Journal of Statistics*, 5, 57-60.

- Labonne, B. (1999) The mining industry and the community: joining forces for sustainable social development. *Natural Resources Forum*, 23, 315–322.
- Lacy, R.C. (2000) Use of population viability analyses in conservation planning. *Ecological Bulletins*, 48, 191–203.
- Lagarde, F., Bonnet, X., Corbin, J., Henen, B., Nagy, K., Mardonov B. & Naulleau, G. (2003) Foraging behaviour and diet of an ectothermic herbivore: *Testudo horsfieldi*. *Ecography*, 26, 236–242.
- Lamoreux, J., Akcakaya, H.R., Bennun, L., Collar, N.J., Boitani, L., Brackett, D., Brautigam, A., Brooks, T.M., de Fonseca, G.A.B., Mittermeier, R.A., Rylands, A.B., Gardenfors, U., Hilton-Taylor, C., Mace, G., Stein, B.A., & Stuart, S. (2003) Value of the IUCN Red List. *Trends in Ecology and Evolution*, 18, 214–215.
- Lande, R. (1987) Extinction thresholds in demographic-models of territorial populations. *American Naturalist*, 130, 624–635.
- Lebreton, J.D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, 62, 67–118.
- Lefkovich, L.P. (1965) The study of population growth in organisms grouped by stages. *Biometrics*, 21, 1–18.
- Leguat, F. (1708) *Voyages et Aventures de François Leguat & de ses Compagnons, en Deux Isles Desertes des Indes Orientales*. Jean Louis de Lorme, Amsterdam, The Netherlands.
-

- Leuteritz, T. & Walker, R. (2009) *Pyxis arachnoides*. *IUCN Red List of Threatened Species* v 2011.2. www.iucnredlist.org. [accessed 22 June 2009].
- Leuteritz, T., Randriamahazo, H. & Lewis, R. (2009) *Pyxis planicauda*. *IUCN Red List of Threatened Species* v 2011.2. www.iucnredlist.org. [accessed 22 June 2009].
- Leuteritz, T.E.J., Lamb, T. & Limberaza, J.C. (2005) Distribution, status and conservation of radiated tortoises (*Geochelone radiata*) in Madagascar. *Biological Conservation*, 124, 451–461.
- Loehr, V.J.T. (2002) Population characteristics and activity patterns of the Namaqualand speckled padloper (*Homopus signatus signatus*) in the early spring. *Journal of Herpetology* 36, 378-389.
- Loehr, V.J.T. (2005) Preliminary results of a long-term field study on the Namaqualand speckled padloper, *Homopus signatus signatus*. *Emys*, 12, 4-17.
- Loehr, V.J.T. (2006) Natural diet of the Namaqualand speckled padloper (*Homopus signatus signatus*). *Chelonian Conservation and Biology*, 5, 149-152.
- Loehr, V.J.T. (2008) *The ecology of the world's smallest tortoise, Homopus signatus signatus: effects of rainfall*. PhD dissertation. University of the Western Cape, South Africa.
- Loehr, V.J.T. (2010) Structure and dynamics of a Namaqualand speckled tortoise (*Homopus signatus signatus*) population over 5 years of rainfall variation. *Chelonian Conservation and Biology*, 9, 223-230.
-

- Lowry, P.P., Schatz, G.E. & Phillipson, P.B. (1997) The classification of natural and anthropogenic vegetation in Madagascar. In: *Natural Change and Human Impact in Madagascar*. (eds S.M. Goodman & B.D. Patterson). Smithsonian Institution Press, Washington D.C., USA.
- Mace, G., Gittleman, J., & Purvis, A. (2003) Preserving the tree of life. *Science*, 300, 1707–1709.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83, 2248–2255.
- Macphee, R.D.E. & Marx, P.A. (1997) The 40,000 year plague: human, hyperdisease, and first-contact extinctions, In *Natural Change and Human Impact in Madagascar*. (eds S.M. Goodman & P.D. Patterson), pp. 169-217. Smithsonian Institution Press, Washington, USA
- Martin, P. & Bateson, P. (1993) *Measuring Behaviour; An Introductory Guide*. Cambridge University Press, Cambridge, UK.
- Martin, P.S. (1966) Africa and Pleistocene overkill. *Nature*, 212, 339-342.
- Mather, P. (1999) *Computer Processing of Remotely Sensed Images: An Introduction*. Wiley-Blackwell, Chichester, UK.
-

- McCoy, E.D., Stys, B. & Mushinsky, H.R. (2002) A comparison of GIS and survey estimates of Gopher Tortoise habitat and numbers of individuals in Florida. *Chelonian Conservation Biology*, 4, 472-478.
- McGowan, P., Gillman, M. & Dodd, M. (1998) Assessing the status of poorly known species: lessons from partridges and pheasants of southeast Asia. *Biological Conservation*, 83, 1-7.
- McKinney, M. L. (1999) High rates of extinction and threat in poorly studied taxa. *Conservation Biology*, 13, 1273-1281.
- Mills, L. S., Doak, D. F. & Wisdom, M. J. (1999). Reliability of conservation actions based on elasticity analysis of matrix models. *Conservation Biology*, 13, 815-829.
- Mittermeier, R.A., Rhodin, A.G.J., Randriamahazo, H., Lewis, R.E., van Dijk, P.P., Hudson, R., and Rioux Paquette, S. (2008) Vision sokatra gasy—Madagascar turtle vision. *Turtle and Tortoise Newsletter*, 12, 7-9.
- Mohan,V. (2009) *Velondriake Region Sexual and Reproductive Health Service Project: 2 Year Report*. Unpublished Report. Blue Ventures Conservation, London, UK.
- Morrow, J.L., Howard, J.H., Smith, S.A. & Poppel, D.K. (2001) Home range and movements of the bog turtle (*Clemmys muhlenbergii*) in Maryland. *Journal of Herpetology*, 35, 68-73.
- Mrosovsky, N. & Godfrey, M.H. (2008) The path from grey literature to red lists. *Endangered Species Research*, 6, 185-191.
-

- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities, *Nature* 403, 853-858.
- Newey, S., Bell, M. Enthoven, S. & Thirgood, S. (2003) Can distance sampling and dung plots be used to assess the density of mountain hares *Lepus timidus*? *Wildlife Biology*, 9, 185-192.
- Nijman, V. & Shepherd, C.R. (2007) Trade in non-native, CITES-listed, wildlife in Asia, as exemplified by the trade in freshwater turtles and tortoises (Chelonidae) in Thailand. *Contributions to Zoology*, 76, 207-212
- North-Coombes, A. (1971) *The Island of Rodrigues*. Port Louis Book Printing, Port Louis, Mauritius.
- Novotny, N., Basset, Y., Miller, S.E., Weiblen, G.D., Bremer, B., Cizek, L. & Drozd P. (2002) Low host specificity of herbivorous insects in a tropical forest. *Nature*, 416, 841–844.
- O'Brien, S, Emahalala, E.R., Beard, V., Rakotondrainy, R.M., Reid, A., Raharisoa, V. & Coulson, T.(2003) Decline of the Madagascar radiated tortoise (*Geochelone radiata*) due to overexploitation, *Oryx*, 37, 338–343.
- O'Brien, S, Bourou, R, Tiandray, H. (2005) Hatch size, somatic growth rate and size dependent survival in the endangered ploughshare tortoise. *Biological Conservation*. 126:141–145.
- Pedrono, M. (2008) *The Tortoises and Turtles of Madagascar*. Natural History Publications (Borneo), Kota Kinabalu, Malaysia.
-

- Pedrono, M., Smith, L.L., in press. Overview of the natural history of Madagascar's endemic tortoises and freshwater turtles: essential components for effective conservation. In *Turtles on the Brink in Madagascar; Proceedings of Two Workshops on Status and Conservation of Malagasy Tortoises and Freshwater Turtles* (eds Castellano, C.M., Randriamahazo, H., Lewis, R.E., Mittermeier, R.A., Hudson, R. & Rhodin, A.G.J.). Chelonian Research Monographs, Lunenburg, MA, U.S.A.
- Perälä, J. (2003) *Testudo kleinmanni*. In *IUCN Red List of Threatened Species*. v 2011.2. <https://www.iucnredlist.org>. [access 18 June 2012].
- Pike, D.A., Pizzatto, L., Pike, B.A., & Shine, R. (2008) Estimating survival rates of uncatchable animals: the myth of high juvenile mortality in reptiles. *Ecology*, 89, 607–611.
- Platt, S.G., Ko, W.K., Khaing, L.L., Myo, K.M., Swe, T., Lwin, T. & Rainwater, T.R. (2003) Population status and conservation of the Critically Endangered Burmese star tortoise *Geochelone platynota* in central Myanmar. *Oryx*, 37, 464–471.
- Rabearivony, J., Thorstrom, R., Rene de Roland, L.A., Rakotondratsima, M., Andriamalala, T.R.A., Sam, T.S., Razafimanjato, G., Rakotondravony, D., Raselimanana, A.P. & Rakotoson, M. (2010) Protected area surface extension in Madagascar: Do endemism and threatened species remain useful criteria for site selection? *Madagascar Conservation & Development*, 5, 35–47.
- Rabesahala Horning, N. (2003). How rules affect conservation outcomes. In *The Natural History of Madagascar* (eds S.M. Goodman & J.P. Benstead), pp. 146–153. University of Chicago Press, Chicago, Illinois, USA.

- Rafeliarsoa, T.H., Shore, G.D., McGuire, S.M. & Louis Jr, E.E. (2010) Innovative Solutions to conservation challenges for the radiated tortoise (*Astrochelys radiata*) project at Lavavolo Classified Forest, Madagascar. *Turtle Survival Magazine*, August 2010, 64-66.
- Randriamahazo, H., Traylor-Holzer, K., Leus, K. & Byers, H.O. (2007) *Population and Habitat Viability Assessment Workshop for Endemic Tortoise Species in Madagascar Geochelone radiata (Madagascar radiated tortoise) Pyxis arachnoides (spider tortoise)*. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN, USA
- Raxworthy, C. & Nussbaum, R. (2000) Extinction and extinction vulnerability of amphibians and reptiles in Madagascar. *Amphibian & Reptile Conservation*, 2, 15-23.
- Raxworthy, C.J. & Nussbaum, R.A. (1996) Montane amphibian and reptile communities in Madagascar. *Conservation Biology*, 10, 750-756.
- Rhodin, A.G.J., Walde, A.D., Horne, B.D., van Dijk, P.P., Blanck, T., & Hudson, R. (eds.) (2011) *Turtles in Trouble: The Worlds 25+ Most Endangered Tortoises and Freshwater Turtles-2011*. IUCN/SSC Tortoise and Freshwater Turtle Specialist Group, Lunenburg, MA, USA.
- Rioux Paquette, S., Behncke, S.M., O'Brien, S.H., Brenneman, R.A., Louis Jr., E.E., & Lapointe, F.-J. (2007) Riverbeds demarcate distinct conservation units of the radiated tortoise (*Geochelone radiata*) in southern Madagascar. *Conservation Genetics*, 7, 297-307.
-

- Rivera-Milan, F.F., Zaccagnini, M.E. & Canavelli, S.B. (2004) Field trials of line-transect surveys of bird carcasses in agro-ecosystems of Argentina's pampas region. *Wildlife Society Bulletin*, 32, 1219-1228.
- Russello, M. A., Glaberman, S., Gibbs, J.P., Cruz, M., Powell, J. R., & Caccone, A. (2005) A cryptic taxon of Galapagos tortoise in conservation peril. *Biological Letters*, 1, 287–290.
- Sarrasin, B. (2006) The mining industry and the regulatory framework in Madagascar: Some developmental and environmental issues. *Journal of Cleaner Production*, 14, 388-396.
- Schowengerdt, R.A. (1997) *Remote Sensing: Models and Methods for Image Processing* (2nd ed). Academic Press, London, UK.
- Scott, D. M., Brown, D., Mahood, S., Denton, B., Silburn, A. & Rakotondraparany, F. (2006) The impacts of forest clearance on lizard, small mammal, and bird communities in the arid spiny forest, southern Madagascar. *Biological Conservation*, 127, 72-87.
- Scott, D., Andriambolanoro, O.A., Mbohoahy, T., Raharinirina, N.C., Smith, M., Tanteliniaina, S., Thompson, S., Tsagnangara C. (2008) University of Brighton Spiny Forest Research Expedition 2007/08: Final Report. Unpublished Report. University of Brighton, UK.
- Scott, J.M., Davis, F.W., Csuti, B., Noss, R., Butterfield, B., Groves, C., Anderson, H., Caicco, S., Derchia, F., Edwards, T.C., Ulliman, J. & Wright, R.G. (1993) Gap analysis: a geographic approach to protection of biological diversity. *Wildlife Monographs*, 123, 1–41.
-

- Seddon, N., Tobias, J., Yount, J.W., Ramanampamonjy, J.R., Butchart, S & Randrianizahana, H. (2000) Conservation issues and priorities in the Mikea Forest of South-west Madagascar. *Oryx*, 34, 287–304.
- Seidensticker, J. (1987) Bearing witness: observations on the extinction of *Panthera tigris balica* and *Panthera tigris sondaica*. In *Tigers of the world: the biology, biopolitics, management, and conservation of an endangered species*. pp. 265–286. (eds R.L. Tilson & U.S. Seal). William Andrew Inc. Norwich, New York, USA.
- Seminoff, J.A., Shanker, K. (2008) Marine turtles and IUCN Red Listing: a review of the process, the pitfalls, and novel assessment approaches. *Journal of Experimental Marine Biology and Ecology*, 356, 52–68.
- Simberloff, D. (1998) Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biological Conservation*, 83, 247–257.
- Smallwood, K.S., Beyea, J.B & Morrison, M. (1999) Using the best scientific data for endangered species conservation. *Environmental Management*, 24, 421–435.
- Smolensky, N. & Fitzgerald, L.A. (2010) Distance sampling underestimates population densities of dune-dwelling lizards. *Journal of Herpetology*, 44, 372–381.
- Stork, N. E. (1993) How many species are there? *Biodiversity and Conservation*, 2, 215–232.
- Swann, D.E., Averill-Murray, R.C. & Schwalbe, C.R. (2002) Distance sampling for sonoran desert tortoises. *Journal of Wildlife Management*, 66, 969–975.
-

- Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J. R., Marques, T.A. & Burnham, K.P. (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, 47, 5–14.
- Thorsen, M., Shorten, R., Lucking, R., & Lucking, V. (2000) Norway rats (*Rattus norvegicus*) on Frégate Island, Seychelles: the invasion; subsequent eradication attempts and implications for the island's fauna. *Biological Conservation*, 96, 133-138.
- Tilman, D.M., Lehman, R.M., Nowak, C.L. & Martin A. (2002) Habitat destruction and the extinction debt. *Nature*, 371, 65 – 66.
- Turner, F.B., Berry, K.H., Burge, B.L., Hayden, P., Nicholson, L. & Bickett, J. (1987) Population ecology of the desert tortoise at Goffs, San Bernar-dino County, California. *Proceedings of the Desert Tortoise Council*. 1984, 68-82.
- Ustun B, Ekercin, S., Musaoglu N. (2004) A performance analysis of the classification and manual digitising methods for the detection of coastline by using satellite image data. *Remote Sensing in Transition*, 1, 143-148.
- van Dijk, P.P., Iverson, J.B., Shaffer, H.B., Bour, R., & Rhodin, A.G.J. (2011) Turtles of the world, 2011 update: annotated checklist of taxonomy, synonymy, distribution, and conservation status. In Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs No. 5 (eds Rhodin, A.G.J., Pritchard, P.C.H., van Dijk, P.P., Saumure, R.A., Buhlmann, K.A., Iverson, J.B., & Mittermeier, R.A.), pp. 000.165–
-

000.242, doi:10.3854/crm.5.000.checklist.v4.2011, <http://www.iucn-tftsg.org/cbft/> accessed 3rd June 2012].

Veiga, M.M. & Hinton, J.J. (2002) Abandoned artisanal gold mines in the Brazilian Amazon: A legacy of mercury pollution. *Natural Resources Forum*, 26, 15–26.

Vieites, D.R., Wollenberg, K. C. Andreone, F. Köhler, J. Glaw, F. & Vences, M. (2009) Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. *Proceedings of the National Academy of Sciences of the USA*, 106, 8267-8272.

Walker, R.C.J & Rafeliasoa, T.H. (2010) Distribution of the Madagascar spider tortoise, *Pyxis arachnoides*. *Turtle Survival Alliance News*, 2010, 61-63.

Walker, R.C.J. & Rafeliasoa, T.H. (2012) Status of the relict population of the Critically Endangered Madagascar spider tortoise *Pyxis arachnoides*. *Oryx*, 46, 453-463.

Walker, R.C.J. (2009) The spider tortoise (*Pyxis arachnoides*): Madagascar's forgotten species? *Testudo*, 7, 77–84.

Walker, R.C.J. (2010) The decline of the northern Madagascar spider tortoise (*Pyxis arachnoides brygooi*). *Herpetologica*, 6, 411-417.

Walker, R.C.J. (2012) A critical evaluation of field survey methods for establishing the range of a small, cryptic tortoise: (*Pyxis arachnoides*). *Herpetological Journal*, 22, 7-12.

Walker, R.C.J., Gardner, J.C., Rafeliasoa, T.H., Smith, I & Razafimanatsoa, R. (in press) Conservation of the Madagascar Spider Tortoise (*Pyxis arachnoides*) amid changing land

use policy: Assessing the spatial coincidence of relict populations with protected areas and mining concessions. In *Turtles on the Brink in Madagascar; Proceedings of Two Workshops on Status and Conservation of Malagasy Tortoises and Freshwater Turtles* (eds Castellano, C.M., Randriamahazo, H., Lewis, R.E., Mittermeier, R.A., Hudson, R. & Rhodin, A.G.J.). Chelonian Research Monographs, Lunenburg, MA, USA.

Walker, R.C.J., Luiselli, L., Woods-Ballard, A.J. & Rix, C.E. (2012a) Microhabitat use by the Critically Endangered Madagascar endemic tortoise, *Pyxis arachnoides*. *Herpetological Journal*, 22, 63-66.

Walker, R.C.J., Luiselli, L & Rafeliarisoa, T.H. (2012b) Survival probability of a population of Madagascar spider tortoises (*Pyxis arachnoides*). *Amphibia Reptilia* 33, 141-144.

Walker, R.C.J., Rix, C.E. & Woods-Ballard, A.J. (2004) The export of the endangered Madagascar spider tortoise (*Pyxis arachnoides*) to support the exotic pet trade. *Herpetological Bulletin*, 90, 2-9.

Walker, R.C.J., Woods-Ballard, A.J., & Rix, C.E. (2007) Population density and seasonal activity of the threatened Madagascar spider tortoise (*Pyxis arachnoides arachnoides*) of the southern dry forests; South West Madagascar. *African Journal of Ecology*, 46, 67-73.

Walker, R.C.J., Whitmore, N., Rafeliarisoa, T.H. & Hamylton, S. (2012c) The effect of habitat deterioration on the long term survival of the Critically Endangered Madagascar spider tortoise. *Biological Conservation*, 152, 152-158.

- White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, 46 (Suppl), 120–138.
- Willemsen, R.E. & Hailey, A. (2001) Variation in adult survival rate of the tortoise *Testudo hermanni* in Greece: implications for evolution of body size. *Journal of Zoology*, 255, 43–53.
- Wilmé, L, Goodman, S.M. & Ganzhorn, J.U. (2006) Biogeographic evolution of Madagascar's microendemic biota. *Science*, 312, 1063-1065.
- Woods-Ballard, A.J. & Fanning, E. (2004) A note on the hunting of radiated tortoises in the Beheloka region, southwest Madagascar. *Turtle and Tortoise Newsletter*, 7, 25-26.
- WWF. (2010) Programme d'actions de WWF sur les tortues terrestres endémiques du sud-ouest de Madagascar: *Astrochelys radiata* et *Pyxis arachnoides* 2010-2015. Unpublished report, WWF, Antananarivo, Madagascar.
- Yakovleva, N. (2005) Corporate Social Responsibility in the Mining Industries. Ashgate Publishing Company, Hampshire, UK.
- Young, R.P., Toto Volahy, A., Bourou, R., Lewis, R., Durbin, J. & Fa, J.E. (2008) Estimating the population of the Endangered flat-tailed tortoise *Pyxis planicauda* in the deciduous, dry forest of western Madagascar: a monitoring baseline. *Oryx*, 42, 252-258.
- Zhou T., McCord, W.P., Blanck, T. & Sun, X-F. (2008) Rediscovery and first breeding of the Yunnan box turtle *Cuora yunnanensis*. *Reptilia*, 59, 29-34.
-

Zwartepoorte, H. (2003) Breeding the Madagascar Spider Tortoise *Pyxis arachnoides*, 1827. In *Madagascar Flat-tailed (Pyxis planicauda) and Spider Tortoise (Pyxis arachnoides) North American Regional Studbook*. 2nd ed. (eds C. Castellano & J.L.Behler), pp 234-245. Wildlife Conservation Society, New York, USA.

Appendix 1.

**Peer review publications resulting from the PhD research currently in print at
the time of submission**
